



First arboreal 'pelycosaurs' (Synapsida: Varanopidae) from the early Permian Chemnitz Fossil Lagerstätte, SE Germany, with a review of varanopid phylogeny

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Abstract

A new fossil amniote from the Fossil Forest of Chemnitz (Sakmarian-Artinskian transition, Germany) is described as *Ascendonanus nestleri* gen. et sp. nov., based on five articulated skeletons with integumentary preservation. The slender animals exhibit a generalistic, lizard-like morphology. However, their synapsid temporal fenestration, ventrally ridged centra and enlarged iliac blades indicate a pelycosaur-grade affiliation. Using a renewed data set for certain early amniotes with a similar typology found *Ascendonanus* to be a basal varanopid synapsid. This is the first evidence of a varanopid from Saxony and the third from Central Europe, as well as the smallest varanopid at all. Its greatly elongated trunk, enlarged autopodia and strongly curved unguals, along with taphonomical observations, imply an arboreal lifestyle in a dense forest habitat until the whole ecosystem was buried under volcanic deposits. *Ascendonanus* greatly increases the knowledge on rare basal varanopids; it also reveals a so far unexpected ecotype of early synapsids. Its integumentary structures present the first detailed and soft tissue skin preservation of any Paleozoic synapsid. Further systematic results suggest a varanodontine position for *Mycterosaurus*, the monophyly of South African varanopids including *Anningia* and the distinction of a skeletal aggregation previously assigned to *Heleosaurus*, now renamed as *Microvaranops parentis* gen. et sp. nov.

Keywords Arboreality · Synapsid phylogeny · Adaptation · Cisuralian · Soft tissue preservation · Volcanic taphonomy

Kurzfassung

Basierend auf fünf artikulierten Skeletten mit Hauterhaltung wird ein neuer, fossiler Amniot aus dem Versteinerten Wald von Chemnitz (Sakmarium–Artinskium-Grenzbereich, Deutschland) beschrieben als *Ascendonanus nestleri* gen. et sp. nov. Die schlanken Tiere sind von generalistischer, echsenhafter Gestalt. Demgegenüber zeigen die synapsiden Schläfenfenster, ventral gekantete Zentren und vergrößerte Iliumblätter eine Zugehörigkeit zur Pelycosaurier-Stufe an. Unter Anwendung eines erneuerten Datensatzes für ausgewählte frühe Amnioten ähnlicher Typologie wird *Ascendonanus* zu basalen Varanopiden gestellt. Damit liegt der erste Nachweis eines Varanopiden aus Sachsen und der dritte aus Mitteleuropa vor, zudem der kleinste Varanopide überhaupt. Sein besonders verlängerter Rumpf, vergrößerte Autopodien und stark gekrümmte Krallen sowie taphonomische Beobachtungen legen eine arboreale Lebensweise inmitten eines dichten Waldhabitats nahe, bis das gesamte Ökosystem von vulkanischen Ablagerungen verschüttet wurde. *Ascendonanus* erweitert die Kenntnis der seltenen basalen Varanopiden enorm, zumal er einen bei frühen Synapsiden bisher unerwarteten Ökotyp aufdeckt. Die Integumentstrukturen stellen die ersten detaillierten und durch Weichteile erhaltenen Hautfunde aller paläozoischen Synapsiden dar. Weitergehende systematische Ergebnisse deuten an: eine varanodontine Position für *Mycterosaurus*, die Monophylie

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südafrikanischer Varanopiden einschließlich *Anningia*, sowie die Unterscheidung einer vormals zu *Heleosaurus* gestellten Skelettaggregation, nun benannt als *Microvaranops parentis* gen. et sp. nov.

Schlüsselwörter Arborealität · Synapside Phylogenie · Anpassung · Cisuralium · Weichteilerhaltung · Vulkanische Taphonomie

Introduction

In-situ fossil forests possess overall significance to reveal what ancient ecosystems were assembled of, how they lived and to what degree they captured even climatic and environmental conditions. Although not rare in the Paleozoic, only a few fossil forests provide more than a witness to the diverse plant life but also to animals and the interactions between various organisms (Shear et al. 1987; Scott 2001; Stein et al. 2012). So-called T⁰ assemblages, instantaneous records from the geologic past (see DiMichele and Falcon-Lang 2011), offer exceptionally detailed pictures of ancient communities and yield not only the potential to reconstruct taphonomical processes but also to understand paleoecologic relationships and whole ecosystems in particular (Appleton et al. 2011; Wang et al. 2012; Opluštil et al. 2014; Berry and Marshall 2015; Falcon-Lang et al. 2016).

Although known since at least the early eighteenth century (Frenzel 1759; Sterzel 1875), the Chemnitz Fossil Lagerstätte only recently attracted broad international interest because of ongoing excavation activities with numerous ground-breaking finds including the first animal remains. After a few selected studies highlighting the largest calamitalean (Feng et al. 2012; Rößler et al. 2012a) and its rooting system (Rößler et al. 2014), the youngest trigonotarbid arachnid known so far (Dunlop and Rößler 2013), the first complete scorpions from the Permian (Dunlop et al. 2016) or paleoclimatic and site-specific conditions of this fossil ecosystem in general (Luthardt et al. 2016; Luthardt and Rößler 2017), we continue to examine additional new finds and their environmental and evolutionary implications. The presence of organisms preserved at this site seems to reflect a relatively young, but already well-established ecosystem with a remarkably developed trophic pyramid (Luthardt et al. 2016).

Within this taphocoenosis, a slenderly built amniote has been found to be the most abundant vertebrate, with a total of five articulated individuals. With respect to their close association to different trees and the enormous curvature of the ungual phalanges, these animals with a lizard-like appearance were seemingly arboreal. During the first closer study, their synapsid nature was recognized. The new taxon described here is the third central-European member of the Varanopidae, besides two Thuringian taxa, *Tambacarnifex*

(Berman et al. 2014) and an indeterminate slender form (Spindler and Werneburg 2016). Its greatest significance arises from the suggested arboreal lifestyle, representing an eco-type that was completely unknown in pelycosaurian-grade synapsids so far.

A list of European pelycosaur-grade synapsids is provided by Fröbisch et al. (2011, appendix 1). In addition, a few more statements are possible. The Russian Mezen fauna has produced the varanopids *Mesenosaurus* (Reisz and Berman 2001) and *Pyozia* (Anderson and Reisz 2004), as well as the caseids *Ennatosaurus* (Maddin et al. 2008) and *Phreato-phasma* (Brocklehurst and Fröbisch 2017). Moreover, there are sphenacodontid fragments from France (Heyler 1969: pl. LII, fig. 7; Falconnet 2013). Fragmentary edaphosaurid spines were described by Prantl (1943).

Subsequent to Fröbisch et al. (2011), the list of European ‘pelycosaurs’ can be extended as follows: (1) *Datheosaurus* and *Callibrachion*, previously mistaken as basal sphenacodontians, have been recognized as basal Caseosauria or Caseidae (Spindler et al. 2016); (2) further renaming or first description of caseids applied to *Euromycter* and *Ruthenosaurus* (Reisz et al. 2011a), as well as *Alierasaurus* (Ronchi et al. 2011; Romano and Nicosia 2014). A large but undescribed caseid is known from the Lopingian of the Lodève Basin (Schneider et al. 2006; Werneburg et al., in prep.). Less derived caseid skeletons from the Tambach Formation (Kungurian, Thuringian Forest Basin) are awaiting their description (Reisz and Fröbisch 2014). (3) The Tambach varanopine varanopid has been described as *Tambacarnifex* (Berman et al. 2014). An undescribed interclavicle from the same locality is indistinguishable from that of *Varanops* (pers. obs. F.S. 2015). (4) A new edaphosaurid has been recovered from the Remigiusberg Formation (Gzhelian?, Saar-Nahe Basin), Germany (Voigt et al. 2014), currently under description and comparison with a potential second edaphosaurid specimen from the Niederhäslich Formation, Sakmarian, Döhlen Basin (pers. obs. F.S. 2016). (5) A revision of basal Sphenacodontia (Spindler 2015) raised doubt about the assignment of cf. *Haptodus* from the Manebach Formation, Asselian, Thuringian Forest Basin (Werneburg 1999) and contains a re-evaluation of ‘*Haptodus*’ *grandis* from the Kenilworth Sandstone Formation, Cisuralian, Pennine Basin, England (Paton 1974; Spindler 2015). (6) Another slender varanopid (Spindler and Werneburg

2016), along with further amniote remains, was collected from the Goldlauter Formation, Sakmarian, Thuringian Forest Basin.

In general, previously known basal synapsids from Europe strongly resemble their counterparts from North American localities. Due to the exceptional habitat unearthed in Chemnitz, the new varanopid displays a form that lacks a closer relative in terms of lifestyle and adaptation.

Institutional abbreviations used in the present study are (including Online Resources): **BP**—Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; **FMNH**—Field Museum of Natural History, Chicago, Illinois, USA; **MCZ**—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MNC**—Museum für Naturkunde, Chemnitz, Germany; **NHMS**—Naturhistorisches Museum Schloss Bertholdsburg Schleusingen, Germany; **OMNH**—Oklahoma Museum of Natural History, Norman, Oklahoma, USA; **PIN**—Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **SAM**—Iziko South African Museum, Cape Town, South Africa; **SNSD**—Senckenberg Naturhistorische Sammlungen Dresden, Germany; **TMM**—Texas Memorial Museum, University of Texas, Austin, USA.

Anatomical abbreviations used in figure captions of this article: *a* angular, *ar* articular, *as* astragalus, *atl* atlas, *ax* axis, *boc* basioccipital, *c* vertebra centrum, *cal* calcaneus, *ce* central, *cer* cervical rib, *cl* clavicle, *cor* coracoid, *cr* caudal rib, *d* dentary, *ec* ectopterygoid, *eoc* exoccipital, *f* femur, *fi* fibula, *fr* frontal, *h* humerus, *hy* hyoid, *icl* interclavicle, *il* ilium, *is* ischium, *j* jugal, *l* lacrimal, *mx* maxilla, *n* nasal, *op* opisthotic, *OR* orbita, *p* parietal, *pal* palatine, *pbsph* parabasisphenoid, *pm* premaxilla, *po* postorbital, *poc* paroccipital process, *pof* postfrontal, *pp* postparietal, *prf* prefrontal, *pt* pterygoid, *pu* pubis, *q* quadrate, *qj* quadratojugal, *ra* radius, *rad* radiale, *sa* surangular, *soc* supraoccipital, *sq* squamosal, *sr* sacral rib, *st* supratemporal, *sta* stapes, *scl.oss* scleral lid ossicles, *scl.pl* scleral ring plates, *t* tabular, *ti* tibia, *ul* ulna, *ule* ulnare, *v* vomer.

Materials and methods

The fossils reported here were found within a few years at the excavation Chemnitz-Hilbersdorf. Due to splitting of the host rock slabs, the dorso-ventrally embedded skeletons show their ventral and dorsal portions each with an exposition of interior parts. All specimens are composed of articulated skeletons with associated skin preservation, representing the first definite soft tissue conservation of any pelycosaur-grade synapsid. The bones are affected by multiple diagenetic processes and modern weathering, resulting in a less detailed preservation of major parts of the skeletons.

Few areas of bluish-white bone substance alternate with an iron oxide-dominated composition.

Five individuals are stored in the paleontologic collection of the Museum für Naturkunde Chemnitz. The first was discovered by Volker Annacker on 2009-09-24, collection number MNC-TA0147 (nick-named 'Schnappi'). Subsequent finds are MNC-TA0269 ('Don,' found by Heiko Böttcher 2009-10-15), MNC-TA0906 ('Lotte,' by Anette Hübner 2010-10-23), MNC-TA0924 ('Slusia,' by Sandra Mehlhorn 2010-11-05) and MNC-TA1045 ('Helge,' by Georg Sommer 2011-06-08). All specimens were CT scanned at the Steinmann Institute, University of Bonn, image processing carried out by V.A. After mechanical preparation by Georg Sommer (Naturhistorisches Museum Schleusingen), the specimens were pre-drawn and recognized as varanopids by R.W., then drawn and photographed by F.S. Figures were processed using the Adobe Design Standard Creative Suite.

Geologic setting and taphonomy

Locality, age and paleoenvironment

The Cisuralian Chemnitz Fossil Forest once developed on wet red beds of a distal braidplain of the Leukersdorf Formation (late Sakmarian) in the Chemnitz Basin (Schneider et al. 2012) and was buried largely in growth position during the deposition of volcanic ashes and flows (Röbner et al. 2008). According to recent investigations by Luthardt et al. (2016), the forest ecosystem developed in a low latitude, seasonal tropical, semi-humid local to semi-arid regional climate and was exposed to an estimated annual precipitation of 800–1100 mm. The age of the host rock, the Zeisigwald Tuff within the upper Leukersdorf Formation (Fig. 1) around the Sakmarian-Artinskian boundary, was constrained radiometrically at 290.6 ± 1.8 Ma by SHRIMP U–Pb dating of zircon grains (Röbner et al. 2009).

A first excavation, carried out by the Museum für Naturkunde in the city of Chemnitz (50°51'58.69"N, 12°57'32.54"E) from April 2008 to October 2011, covered an area of 24 m by 18 m and reached a depth of approximately 6 m (Fig. 2). As a result, about 2000 fossils of different preservational states were discovered. For every fossil find coordinates in three-dimensional space were recorded, thus enabling 3D visualization and reconstruction of the in situ forest window (Fig. 3). Among 53 multi-aged stems of medullosan and cordaitalean gymnosperms, calamitaleans and tree ferns, encountered in life position and still rooted in their paleosol, 7 vertebrate skeletons and 11 arthropod remains were found (Röbner et al. 2012b). Biostratigraphical, geologic and taphonomical specifics of the excavation site and the whole fossil Lagerstätte were reported in detail

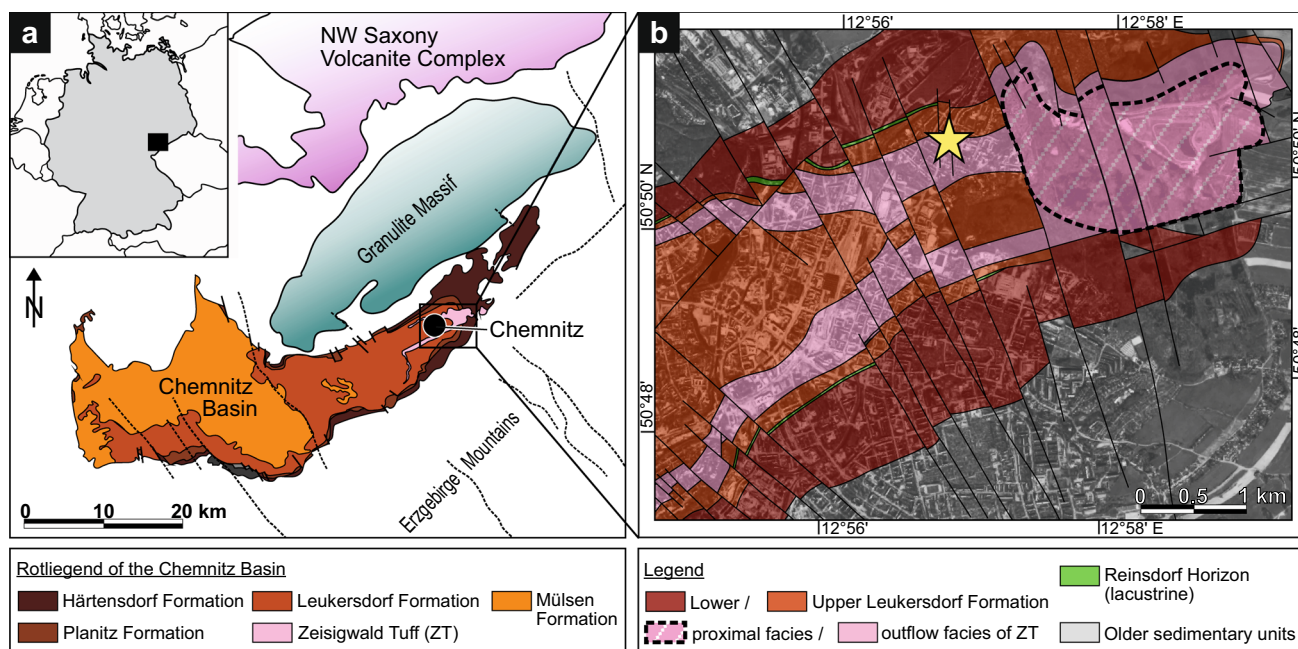


Fig. 1 Geographical position and geologic setting of the Chemnitz Fossil Forest. **a** Geology of central Saxony; study site located in Chemnitz (modified from Schneider et al. 2012). **b** Outcrop of the

Zeisigwald Tuff pyroclastics (ZT) in the settled area of Chemnitz (yellow star: Chemnitz-Hilbersdorf excavation, study site)

by Kretzschmar et al. (2008) and Rößler et al. (2009, 2010, 2012b) and amplified more recently in Luthardt et al. (2016).

Geologic section and depositional facies

The Zeisigwald Tuff, consisting of an about 90 m caldera fill facies and up to 55 m of caldera outflow facies, is restricted to the Chemnitz Basin and can be traced up to a distance of approximately 10 km from the eruption centre. The excavated section of Chemnitz-Hilbersdorf (Fig. 1) is only 500 m away from the caldera border. It has been divided into several units, from the base to the top consisting of the forest's paleosol (Unit S6), the pyroclastic sequence of the Zeisigwald Tuff (units S5–S3) up to the weathered runoff hill scree and the extant soil horizon (units S2 and S1). Here we restrict in-depth information to the strata that yielded animal remains (Fig. 4). For more details see Rößler et al. (2012b) and Luthardt et al. (2016).

Unit S6 represents what we interpret as the vegetation's original substrate, a mineral immature, entisol-like paleosol, lacking features of intense chemical alteration, with diverse rooting structures of the upright-standing hygrophilous arborescent plants (Luthardt et al. 2016). In addition, the paleosol was colonized by several faunal elements. Clusters of terrestrial gastropods were found on the surface of deadwood trunks or around other organic matter. The first complete Permian scorpions and several molting remains of them were discovered in their natural burrows within a plant root

network (Dunlop et al. 2016). A trigonotarbid arachnid and small isolated bones complete the fossil record of the paleosol, which is characterized in detail by Luthardt et al. (2016).

Unit S5 comprising the basal ash tuffs has proven to be the key horizon of the whole fossiliferous section revealing nearly the entire adpression flora and the majority of faunal elements including all vertebrates. It is recognized as a multilayered, thinly bedded succession of ash tuffs, in total 0.53 m thick, and, according to depositional characteristics, it can be subdivided into four different facies (Rößler et al. 2012b). It may have resulted from low-concentration pyroclastic density currents and accompanying fallout that covered the standing vegetation and were caused by an explosive magmatic to phreatomagmatic eruption with activity pulses and a general increase in intensity (Rößler et al. 2012b). Unit S4 represents a roughly 5-cm-thick accretionary lapilli-rich ash tuff. Unit S3 overlies S4 with a sharp erosive base and represents a lapilli-bearing ash tuff with a preserved thickness of 3.35 m. It is interpreted as a hot ignimbritic pyroclastic flow deposit with a high concentration of particles resulting from a phreatomagmatic eruption, which is responsible for the final destruction and burial of the forest ecosystem close to the eruption center.

Taphonomy

The first ash fall resulted in a very fine-grained and dark purple-colored ash tuff deposited directly on the soil surface.

Designated as S 5.0, this unit is only locally distributed and shows varying thicknesses of up to 100 mm. Overprint and delithification can be attributed to sub-recent sliding processes. Nevertheless, this unit contains single glass shards and seems to equalize the morphologic relief of the underlying soil. The following units S 5.1–S 5.3 represent a single eruption event comprising ash falls (S 5.1) and surges (S 5.2, S 5.3). A general coarsening tendency up to the middle of Unit S 5.3 indicates increasing eruption intensity. The fine ash in the uppermost 40 mm of S 5.3 is regarded as accompanying fallout.

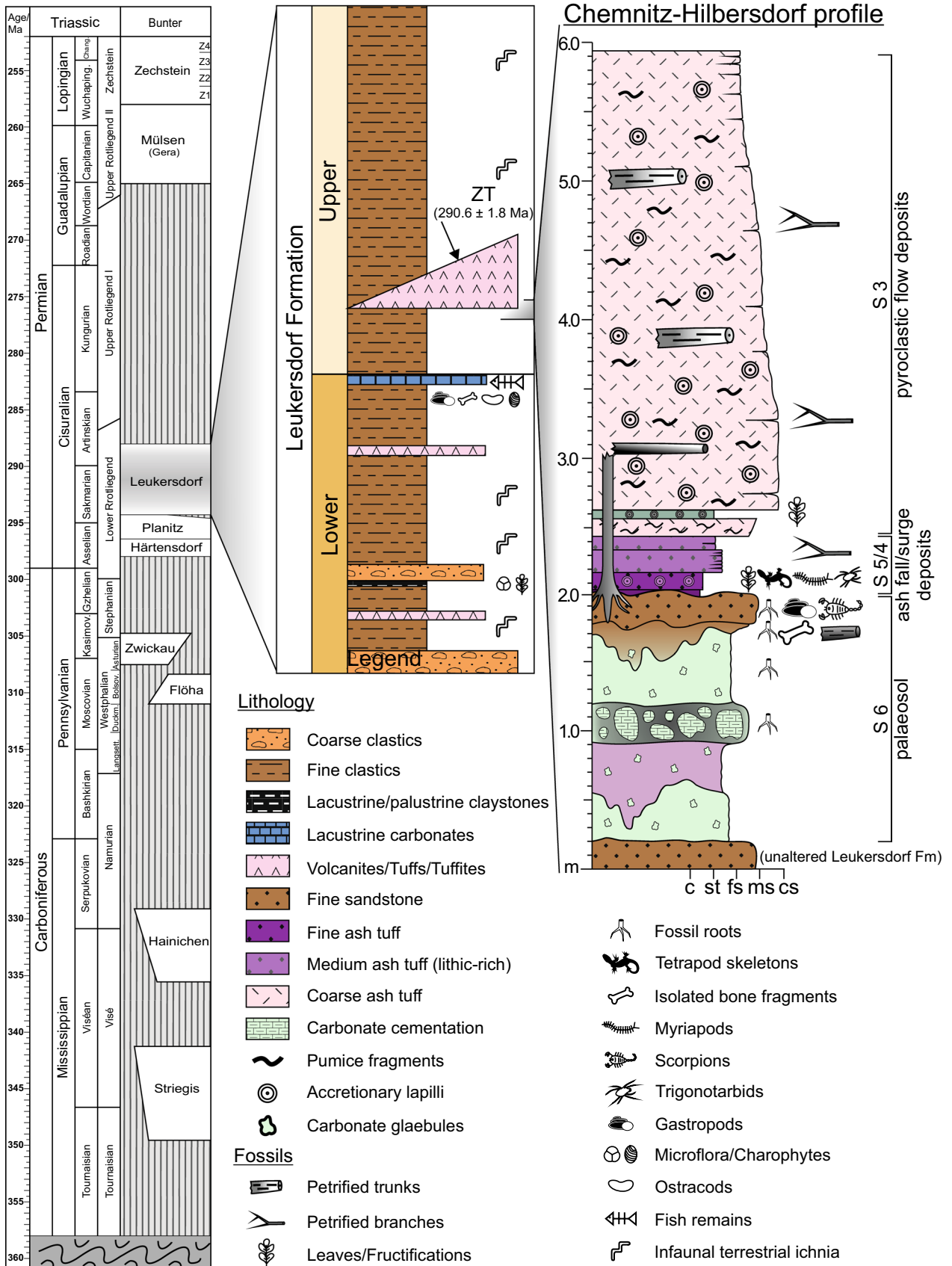
The fossiliferous Unit S 5.1 is approximately 120–200 mm thick and consists of a purple-red, well-sorted, non-welded, accretionary lapilli-bearing fine ash tuff with coarser laminae. At the base a 20-mm-thick coarse layer contains greenish lithic fragments of metamorphites, quartz and feldspar crystals, compacted pumice particles in a size range of 0.4–1.2 mm and isolated accretionary lapilli of 2–3 mm in a dark purple-red matrix consisting mainly of blocky and thin-walled vesicular shards. This lowermost layer contains large quantities of plant adpressions, such as leafy shoots, pinnate frond portions, and detached whole and fragmentary leaves reflecting both in situ and transported vegetational elements (Rößler et al. 2012b; Luthardt et al. 2016). The following layer, a 30-mm fine ash tuff, contains two 1–3-mm-thick laminae very rich in compacted whitish pumice fragments. The base and top show gradual transitions to the dominating fine ash tuff. About 50–60 mm above the base, a second coarser layer follows, about 5 mm thick, and displaying the same composition as the one at the base of Unit S 5.1. The latter layer is the key deposit of this study. Besides rare plant twigs, such as a *Cordaicladus* branch close to MNC-TA0906, it yielded outstanding faunal remains. Among them are diverse vertebrates—comprising the varanopids described here, an aistopod lepospondyl and remains of a probable new temnospondyl. In addition, several invertebrates were found, such as diplopods, one leg of *Arthropleura* and several arachnids including trigonotarbid and one uropygid (Rößler et al. 2012b; Dunlop and Rößler 2013). The remaining 60 mm of ash tuff up to the top of Unit S 5.1 shows an increasing number of accretionary lapilli up to 5 mm in diameter. The top of S 5.1 is terminated by an additional coarse layer of 8 mm thickness, rich in compacted pumice fragments (ca. 50%) up to 3 mm in diameter and a distinct bedding plane as boundary to Unit S 5.2.

With respect to the taphonomy of specimens from the compacted ash tuff, the five varanopids (Figs. 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15) and the temnospondyl are all embedded with their ventral side to the bottom. The varanopids are horizontally buried, except for MNC-TA0924. The head of the latter was found in the level of the coarser lamina, the fore legs slightly higher, the trunk with pelvic girdle and the tail are sunken into the fine ash tuff below. The varanopids

MNC-TA0269, TA0924 and TA0147 exhibit a slight sigmoidal bending (Figs. 5, 7, 9), whereas TA1045 and TA0906 are slightly curved (Figs. 12, 14). All varanopids are somewhat inclined laterally to the left or right, as indicated by the position of the vertebral column in relation to the ribs and the body outline. The hind legs, when preserved, retained a more or less natural posture with the femora placed rectangularly and the remainder leg parallel to the body. The forelegs show varying postures. The phalanges of the right pes of MNC-TA1045 (Fig. 14) are situated about 5–7 mm deeper in the matrix as the remaining skeleton. The unguals of the distally directed right foreleg contact the dorsal side; the wrist of the left foreleg is situated 2–3 mm deeper than the body, the unguals a few millimeters higher. Compared to the body, the phalanges of the left pes of MNC-TA0269 are buried about 3 mm deeper; terminal phalanges of the distally bent forelegs are situated below the venter. The phalanges of the right foreleg of MNC-TA0906 (Fig. 12) are embedded somewhat higher than the remaining skeleton. The left foreleg of TA0924 (Fig. 5) is situated a few millimeters deeper in the matrix than the body; the phalanges of the posteriorly directed right foreleg are situated on the back. The foreleg and the preserved hind leg of TA0147 (Fig. 7) lay in the same level as the body.

Since the coarser layer that yielded the skeletons does not show any indication of disturbance, it is assumed that the vertebrates were unable to move in any way during burial. They were apparently dead or paralyzed at that time. As indicated by the exceptional preservation of the integument, the animals have been embedded without any trace of previous decay. Additionally, there is no evidence of lateral transport of the bodies. If any lateral force had moved the relatively heavy bodies, the coarse particles in the fine ash tuff should display indicative structures such as sorting or flow-generated bedding. However, none of these are proven. The kind of burial, with mainly horizontally laying bodies and extremities sticking deeper into the matrix or bent over the back side, supports the assumption that the animals may have fallen from an elevated position into the ash when they were already dead or at least immobilized. Inclined orientation of some bodies in the matrix may have resulted from oblique orientation during the fall. A drop from the arborescent vegetation seems plausible for the varanopids, which were demonstrably arboreal, as implied by their morphology. Although quite equally distributed over the excavation area, the five recovered varanopid skeletons appear to indicate a relation to larger trees as they were found close to trunks of larger diameters (Fig. 3). Both the ash beds containing vertebrate remains and all larger trees were covered by pyroclastic depositions (S 4–S 3) of more than 3 m distinctly before the tree tops were broken off.

A remaining question refers to the cause of the sudden, nearly contemporaneous death of the animals at some time



◀**Fig. 2** Stratigraphy of the Chemnitz Fossil Forest within the Chemnitz basin. Lithologic section of the Hilbersdorf excavation represents the basal section of the Zeisigwald Tuff pyroclastics (ZT), as part of the upper Leukersdorf Formation, exhibiting a radiometric age of 290.6 ± 1.8 Ma

after the S 5.1 eruption had started. Interpreted as volcanic ash that was deposited during the first fallout from a phreato-plinian eruption, the gradual transitions between the fine ash and coarser laminae point to varying eruption intensities without any clear interruption. Lacking bedding planes and the irregular splitting of Unit S 5.1 additionally underline the assumption that this fossiliferous horizon represents a single volcanic event of relatively short duration. The occurrence of accretionary lapilli reveals the phreatic influence that was already apparent during this very initial eruption stage. Thus, trees partially lost their foliage, which is found embedded in the first centimeters of Unit S 5.1. Leafy twigs and branches broke under the heavy load of depositing ash. Obviously, the animals survived the first eruption phase, but died at the start of the second pulse. Because of the delicate preservation of life-position seed fern organs (Rößler et al. 2012b: fig. 7; Feng et al. 2014: figs. 1–3) and the lack of any charred plant material in S 5.1, the temperature of the ash could hardly have caused the animal's death. The surface of stems and branches frequently preserved a cover rim of fine ash tuff, which may have stuck as a moist adhesive matter. Higher temperatures were probably not reached before Unit S3 entombed the remaining forest (Rößler et al. 2012b). However, the ignition temperature of wood, 280 °C, was obviously never reached during the eruption series at the Chemnitz-Hilbersdorf site. However, even a relatively low temperature of about 50 °C would exceed lethal temperatures for animals (Bradshaw 2003). We rather favor other reasons that may have caused the animal's death, such as the choking fine ash or volcanic gases.

Systematic Paleontology

(unranked) **Synapsida** Osborn, 1903

Family **Varanopidae** Romer and Price, 1940

Remarks. Spelling after Reisz and Dilkes 2003, replacing 'Varanopsidae' (Romer and Price 1940) and 'Varanopseidae' (Langston and Reisz 1981).

Ascendonanus nestleri gen. et sp. nov.

Figures 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26a, 27, 28, 29, 32a, 33a, 34

Etymology. Latin for 'climbing dwarf,' with epithet honoring Mr. Knut Nestler, citizen scientist from Chemnitz, who

passed away in 2016 after decades of friendship and deeply appreciated cooperation with the Chemnitz Museum.

Material. Holotype.—MNC-TA0924 (Figs. 16, 17), chosen for having preserved the most cranial details. Paratypes—MNC-TA0147 (Figs. 18, 19), TA0269 (Figs. 20, 21), TA0906 (Figs. 22, 23), TA1045 (Figs. 24, 25); articulated skeletons and integument.

Locality and horizon. Chemnitz-Hilbersdorf, excavation Frankenberger Straße 61, Saxony, Germany; basal section of Zeisigwald Tuff, Leukersdorf Formation, Rotliegend (Sakmarian-Artinskian transition, Cisuralian), Chemnitz Basin.

Diagnosis. A small and slenderly built, highly autapomorphic varanopid with elongated trunk, lid ossicles in large orbital fenestra; apparently plesiomorphic in exhibiting a small naris, long lacrimal and low maxilla; orbital contribution of frontal restricted, projecting supratemporal forming a rudimentary otic notch, almost homodont dentition, less curved to straight conical teeth that lack serration, single tooth row on pterygoid transverse flange, hyoids shorter than in other varanopids; autapomorphic in a greatly increased number of at least 34 presacral vertebrae; sacral ribs uneven in size, trunk longer than hind limb, subequal lengths of forelimbs and hindlimbs, slender long bones, ectepicondyle foramen on humerus, reduced olecranon, proportionally large autopodia compared to other early synapsids, slender ulnare and calcaneus, perforating foramen restricted to astragalus, slender phalanges; unguals more curved than in any known early synapsid.

Description. From the articulated skeletons, a small and slender-built synapsid can be described. *Ascendonanus* is largely lizard-like in its overall body shape, with a greatly elongated trunk portion. Regarding the below comparative osteology, more detailed comparisons are presented in Online Resource 3, containing comments on the character list and anatomical background for the included characters.

All known specimens of *Ascendonanus nestleri* represent grown individuals, indicated by a finished articular, well-ossified 'epiphyseal' regions of long bones, the complete ossification of the carpus and tarsus and apparently a closed pelvic ventral plate. Adult members of this species measure about 0.4 m in total length, with a greater uncertainty due to missing distal tail portions.

Integument. Integumentary structures are preserved in all specimens, presenting the first detailed and soft tissue skin preservation of any Paleozoic synapsid, as well as one of the oldest known in amniotes. A more exhaustive comparison is subject to a subsequent study. Preliminary observations show a regular scale pattern, which is within the spectrum

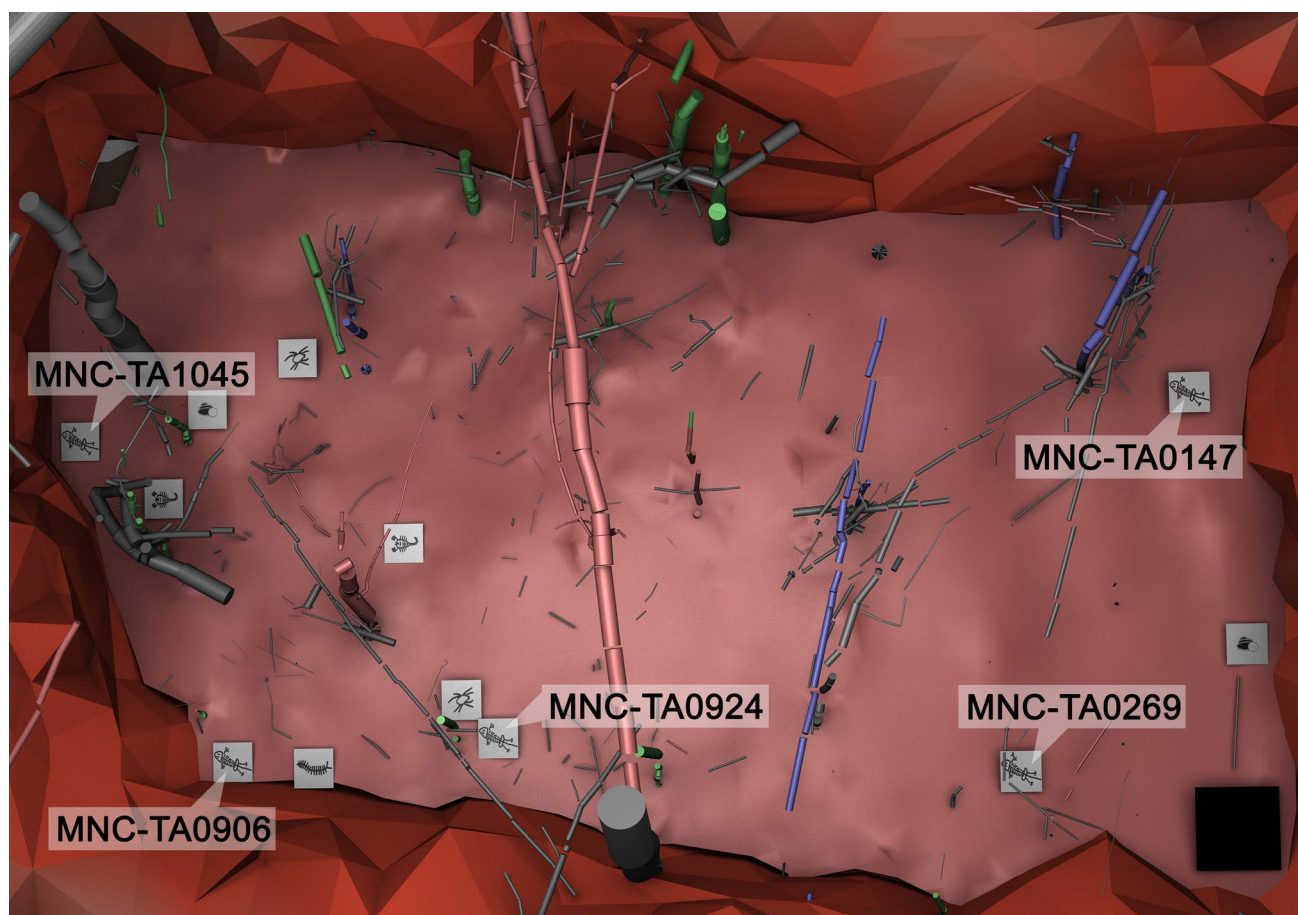


Fig. 3 Three-dimensional plan view model of the excavation at the level of the first ash fall deposit. Tree trunks are shown interspersed with various animal fossils, all presumed to be close to their origi-

nal life position. The original positions of the labeled five varanopid specimens seem to reflect a relation to neighboring larger trees. Black square measures 1×1 m

of extant non-avian reptiles and, therefore, might represent a symplesiomorphy of amniotes. The completeness of integument preservation gives an impression of soft tissue cover around limb bones, as well as of the slender trunk and plump neck.

In the orbits of MNC-TA0924 and TA1045, distinct patches of rounded, polygonal ossicles are preserved as impressions that close with the dorsal orbital rim (Figs. 17, 25). Such ossifications in the dorsal lid are characteristic of certain species and genera of micromelerpetontids and amphibamids as representatives of dissorophoid temnospondyls (Boy 1972: fig. 4q, 1980: fig. 2, 1985: fig. 2, 1995, 2002: fig. 3; Boy and Sues 2000; Broili and Schröder 1937: 23; Credner 1881: 587, 1886: pl. 18, figs. 4–7; Werneburg 1991: figs. 10, 11, 12, 1993: figs. 1, 2). These lid ossicles are clearly distinguished from scleral ring elements (Fig. 26), which are apparently un-ossified in *Ascendonanus*. We could not find any further non-temnospondyle evidence for such a pattern, making the scleral lid ossicles of *Ascendonanus* a unique phenomenon within Amniota. This autapomorphy

raises the question whether it developed independently from Dissorophoidea or was retained throughout a deep homology within a wider tetrapod clade.

No dorsal trunk osteoderms were identified, contrasting with rare varanopid examples (Carroll 1976; Reisz et al. 1998; Botha-Brink and Modesto 2007). Gastralria are indicated in MNC-TA0269 and TA0906. In MNC-TA1045, a set of gastralria follows the ventral line of the preserved integument. However, it could not be observed that the gastralria are built up of internally segmented strings.

Cranial Region. The skull of *Ascendonanus* is slender and sub-triangular (Fig. 27g). Its relative length is reduced, as also seen in caseids and some small varanopids (Online Resource 3: character 2). Due to a rather strong compaction, it cannot be determined whether the skull was as flat in life or markedly taller. The huge orbit is placed a little posterior to the skull mid-length. In the temporal region, the lateral temporal fenestra is similarly built to other small basal varanopids. The zygomatic arc is slender

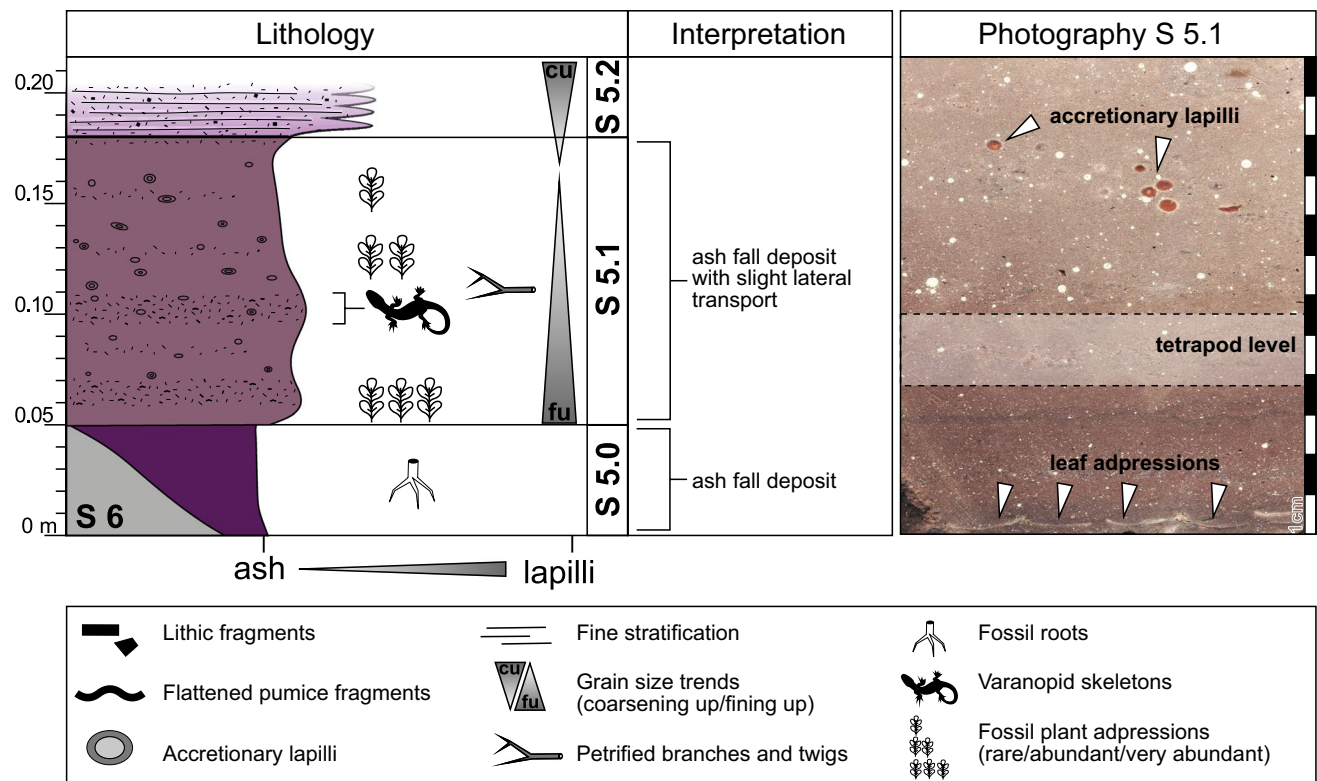


Fig. 4 Detailed profile section of the basal-most pyroclastic units S 5.0–S 5.2 illustrating the taphonomical position of all tetrapod skeletons, which were found in the Chemnitz-Hilbersdorf excavation. The

distinct tetrapod level is characterized by a coarser layer with small pumice and lithic fragments

and straight ventrally. The jaw joint is not placed far posterior to the occipital condyle. However, the slope of the occipital plane is difficult to determine, subject to the orientation of the postparietals in life. Skull ornamentation of tubercles and ridges, present in most varanopids including *Apsisaurus* (Reisz et al. 2010: fig. 1b) is missing. Instead, *Ascendonanus* exhibits small pits on the postfrontal and supratemporal, somewhat resembling the ornamentation of caseasaurians and early eureptiles.

Snout tip—There is no well-preserved snout tip, making it difficult to reconstruct the premaxilla, septomaxilla or narial characteristics. In MNC-TA0924, the premaxillary-maxillary contact was identified anterior to a larger matrix gap, so that there might be about five to six premaxillary teeth and probably four precanine maxillary teeth (Fig. 17). Apparently, the external naris is small (Fig. 27a), unlike the condition in other varanopids.

Maxilla—Ventrally, the maxilla is nearly straight. The shallow dorsal expansion does not contact with the prefrontal. Although it is impossible to determine the exact number of maxillary teeth, it can be reconstructed as being higher than 22. Posteriorly, the tooth row reaches the suborbital area. Weakly enlarged teeth define the caniniform region at about half the antorbital range (Fig. 27c). The double-canine

condition of most early eureptiles and pelycosaur-grade synapsids is absent, reflecting a typical pattern of varanopids (Online Resource 3: character 32).

Lacrimal—The lacrimal is long, apparently reaching from the orbital rim to the external naris. No lateral opening for the lacrimal duct could be identified, contrasting with the condition seen in *Mycterosaurus* (Berman and Reisz 1982) and *Mesenosaurus* (Reisz and Berman 2001).

Prefrontal—On the external skull roof, the prefrontal is smooth, lacking a pocket-like recess. A ventral process constricts the lacrimal contribution to the orbit, which is typical of the included early parareptiles, derived ophiacodontids and non-varanodontine varanopids only.

Frontal—The frontals cover most of the longitudinal range of the orbit, whereas the anterior extent is indistinctly preserved. The lateral edge is almost parasagittal. An inconspicuous lateral lappet in the posterior frontal interrupts the prefrontal-postfrontal margin by a tiny orbital contribution. The posterolateral wings are part of a strongly indented frontal-parietal suture.

Postfrontal—No lateral expansion is visible in the postfrontal, which smoothly continues the concave orbital rim of the prefrontal to postorbital. The medial margin is

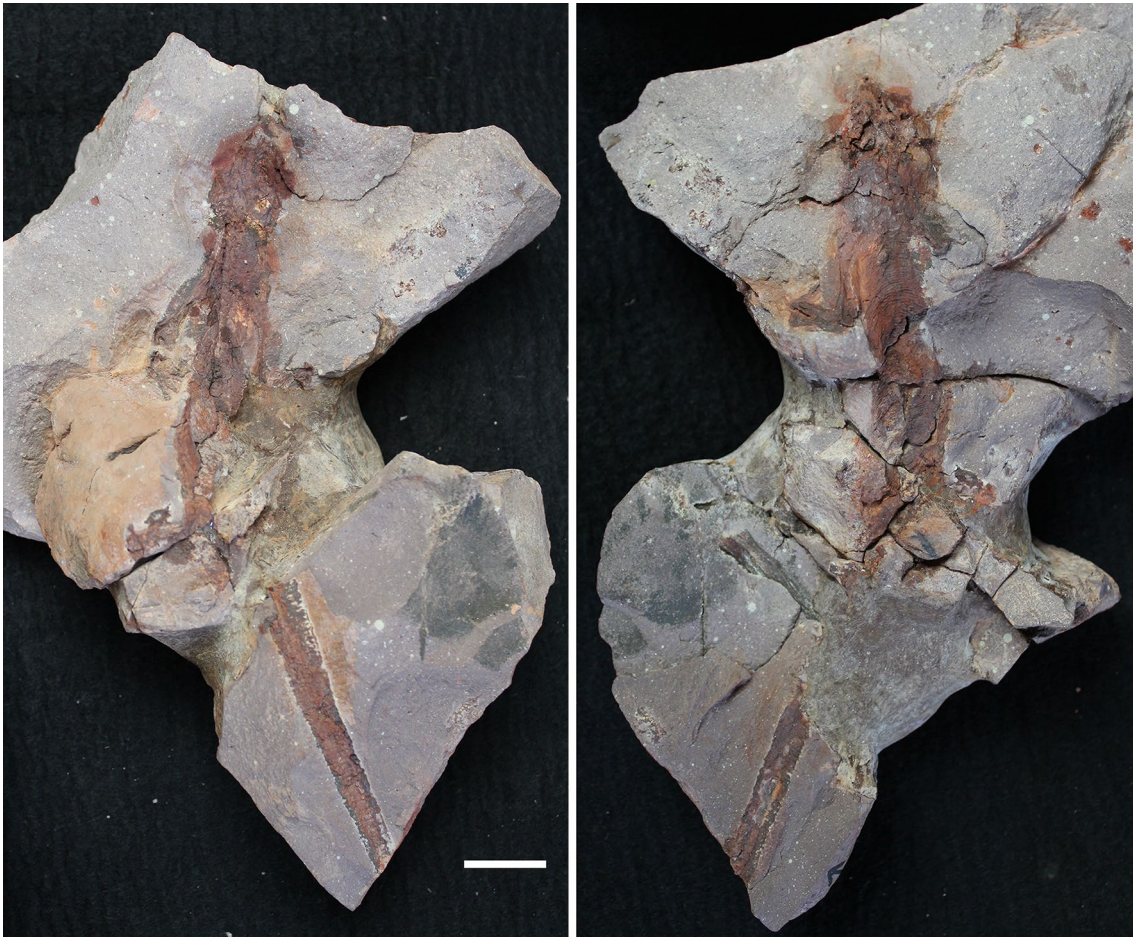


Fig. 5 Counterslabs of MNC-TA0924, holotype of *Ascendonanus nestleri* gen. et sp. nov. Scale bar measures 2 cm

straight to convex, contacting the frontal and parietal by nearly equal portions.

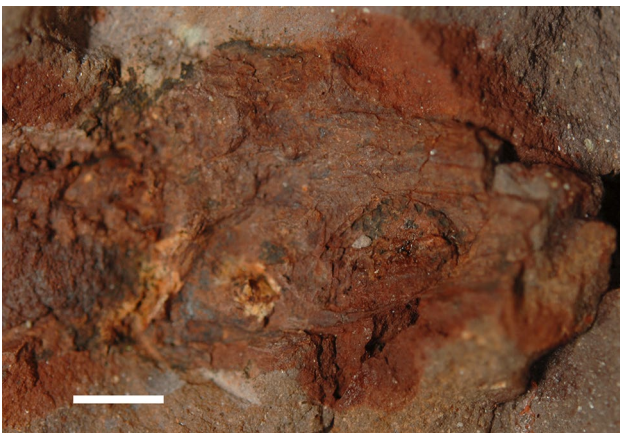


Fig. 6 Close-up of MNC-TA0924, holotype of *Ascendonanus nestleri* gen. et sp. nov., exposing the impression of the skull table. Scale bar measures 5 mm

Jugal—The jugal contributes to the ventral cheek margin. At the anterior tip, the jugal is a slender, pointed splint that covers the suborbital portion of the maxilla. This pattern is typical for caseosaurs and varanopids, but also found in various early reptiles.

Postorbital—As seen in MNC-TA0924 (Fig. 17), the postorbital is triradiate, resembling that of *Archaeovenator* (Reisz and Dilkes 2003). The absence of a lateral boss precludes *Ascendonanus* from the currently known spectrum of “mycterosaurines” (clade designation in quotations because of doubt about the validity, see below). Throughout the dorsal rim of the temporal fenestra, the posterior process of the postorbital is broad. It does not contact the supratemporal.

Parietal—Anteriorly, the parietals extend over the orbit. In the posterior half of the interparietal suture, the parietals enclose a pineal foramen of moderate size, not as enlarged as in caseosaurs and “mycterosaurines.”

Supratemporal—MNC-TA0924 preserves the best supratemporal. It is slender and slightly longer than the distance from the anteriormost point of its parietal groove to the posterior border of the squamosal, producing a weak

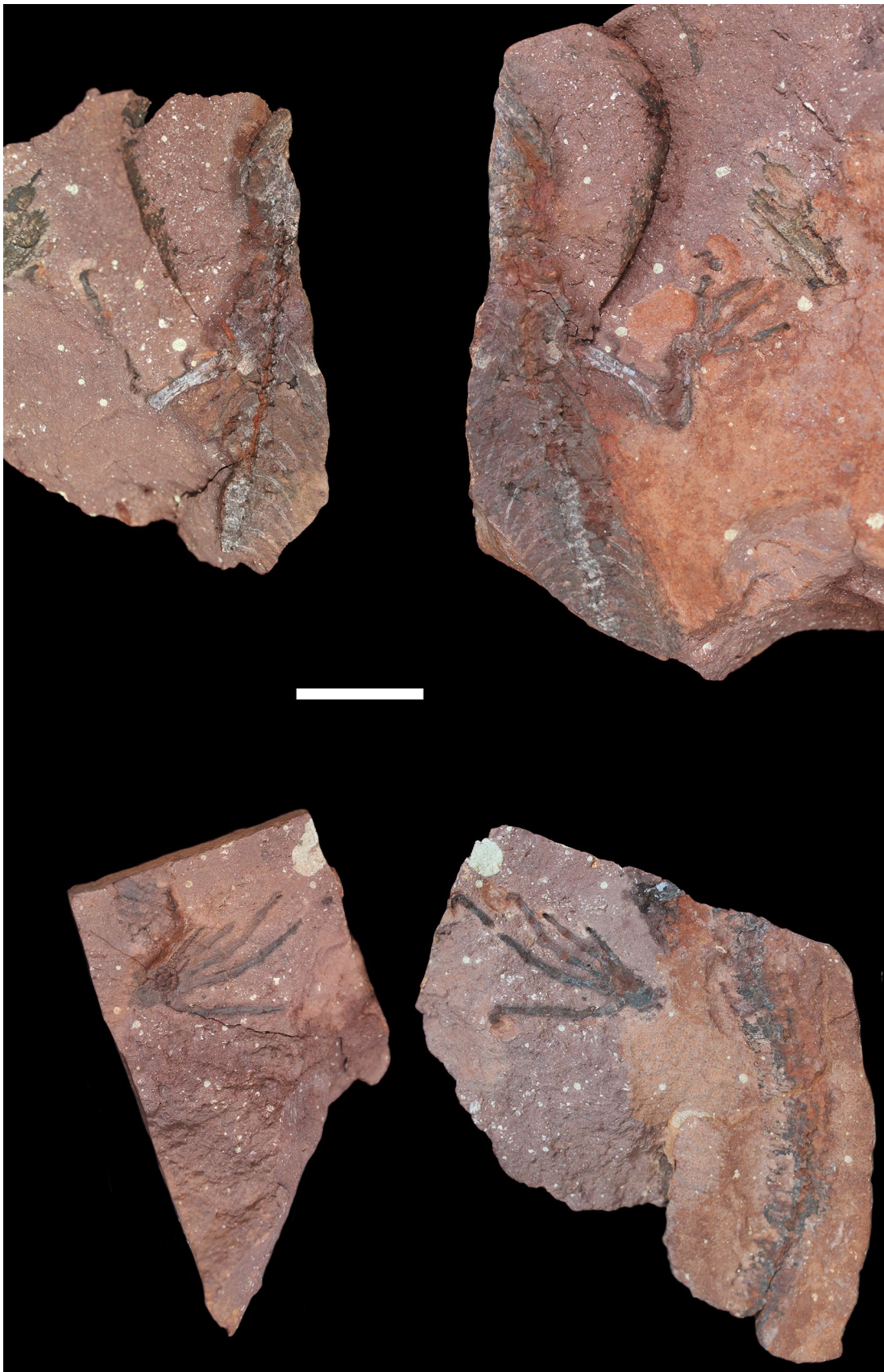


Fig. 7 Counterslab pieces of MNC-TA0147 of *Ascendonanus nestleri* gen. et sp. nov. Scale bar measures 2 cm



Fig. 8 Close-ups of MNC-TA0147 of *Ascendonanus nestleri* gen. et sp. nov., left hind feet of both slabs. Scale bar measures 5 mm

remnant of the otic notch. A similar pattern is also retained in some early reptiles, caseosaurs and at least one other varanopid (Online Resource 3: character 54; Botha-Brink and Modesto 2009: fig. 2).

Squamosal—No ornamentation could be identified on any preserved squamosal. In the lateral aspect, the vertical part is a stout column instead of a broad shield or slender bar. This squamosal outline is indicative of caseosaurs or non-varanodontine varanopids. On the ventral border of the temporal fenestra, the anteroventral process of the squamosal meets the jugal and restricts the quadratojugal from the fenestra. The presence of a posterodorsal process is shared with Caseosauria and “Mycterosaurinae” (Online Resource 3: character 56).

Quadratojugal—The zygomatic process of the quadratojugal is excluded from the temporal fenestra rim. There is no maxillary contact, leaving the jugal to greatly contribute to the ventral border of the upper skull.

Palate—Only limited information can be given on the dermal palate. A row of denticles in MNC-TA0906 (Fig. 23) indicates the position of the vomers. The palatine dentition is a continuation of one of the denticle fields of the anterior ramus of the pterygoid. No ectopterygoid can

be identified with certainty, although possibly preserved in MNC-TA0906. Unfortunately, this specimen reveals no clear suture. Since the ectopterygoid is edentulous in *Archaeovenator*, the denticle rows likely indicated the extension of the palatine. As indicated by MNC-TA0906 and TA0269, the transverse flange of the pterygoid bears a narrow line of denticles not larger than the remainder palatal teeth. The longitudinal level of the transverse flange is at three quarters of the skull length, which is about the level of the postorbital bar.

Occiput and Braincase—The tabulars are slender. The tall postparietals meet in a median ridge, but are seemingly sutured (Fig. 19). Only fragmentary evidence is known from the supraoccipital, exoccipitals, basioccipital or the opisthotic. On the latter, the paroccipital processes are low and restricted in their lateral expansion.

Remains of the parasphenoid are present in some skulls, but the only one revealing certain conditions is MNC-TA0269 (Fig. 21). In rough outlines, the basal plate is subtriangular, contrasting with the trapezoidal shape in *Pyozia* (Anderson and Reisz 2004: fig. 1) and most derived varanopids. The concave lateral edges lack dentition, whereas



Fig. 9 Counterslabs of MNC-TA0269 of *Ascendonanus nestleri* gen. et sp. nov. Scale bar measures 2 cm

the medial part and the basis of the cultriform process bear smaller denticles. This distribution is rather unique or superficially resembles that of varanodontines. There is no median ridge on the basal plate. Like in most varanopids, the basiptyergoid processes are broad and face laterally.

Mandible—As in all varanopids, the mandible is slender. Assuming a continuous tooth row, there are at least

27 dentary teeth (Fig. 27f). Both hemi-mandibles meet in a narrow angle and are straight except for the slightly medially bent posterior portion. The coronoid region is shallowly convex, with its tallest eminence placed far posterior. In the symphysis, the dentary lacks a terminal thickening. The angular as well as the entire mandible ramus bears a sharp ventral edge, but lacks a reflected lamina.

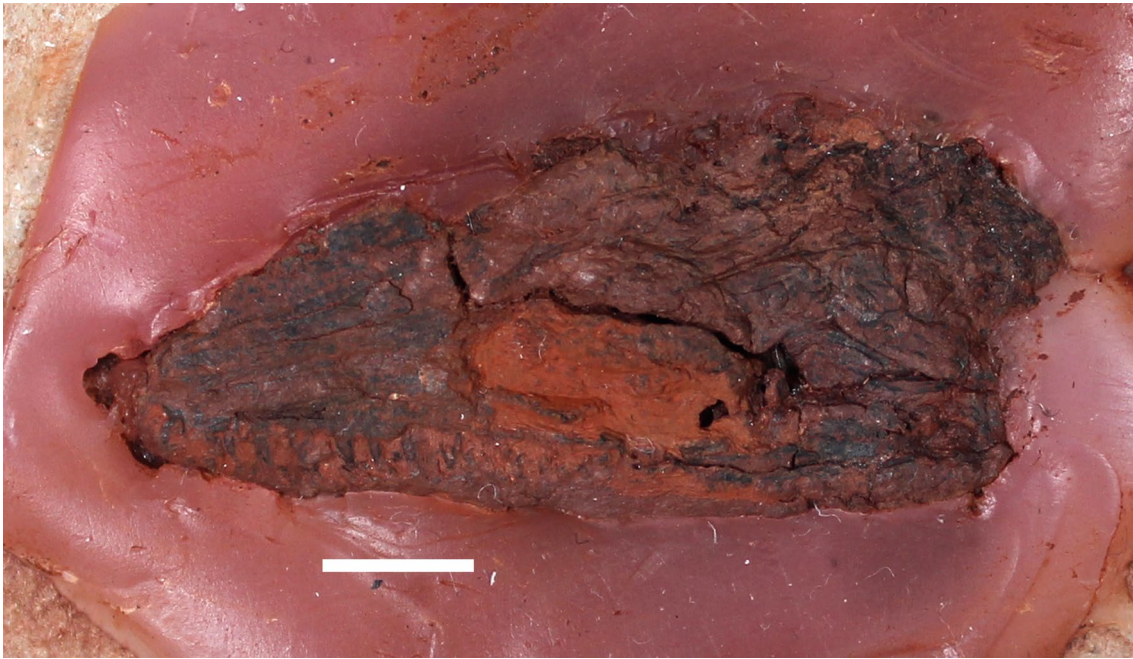


Fig. 10 Removed skull portion of MNC-TA0269 of *Ascendonanus nestleri* gen. et sp. nov., embedded in wax. Scale bar measures 5 mm

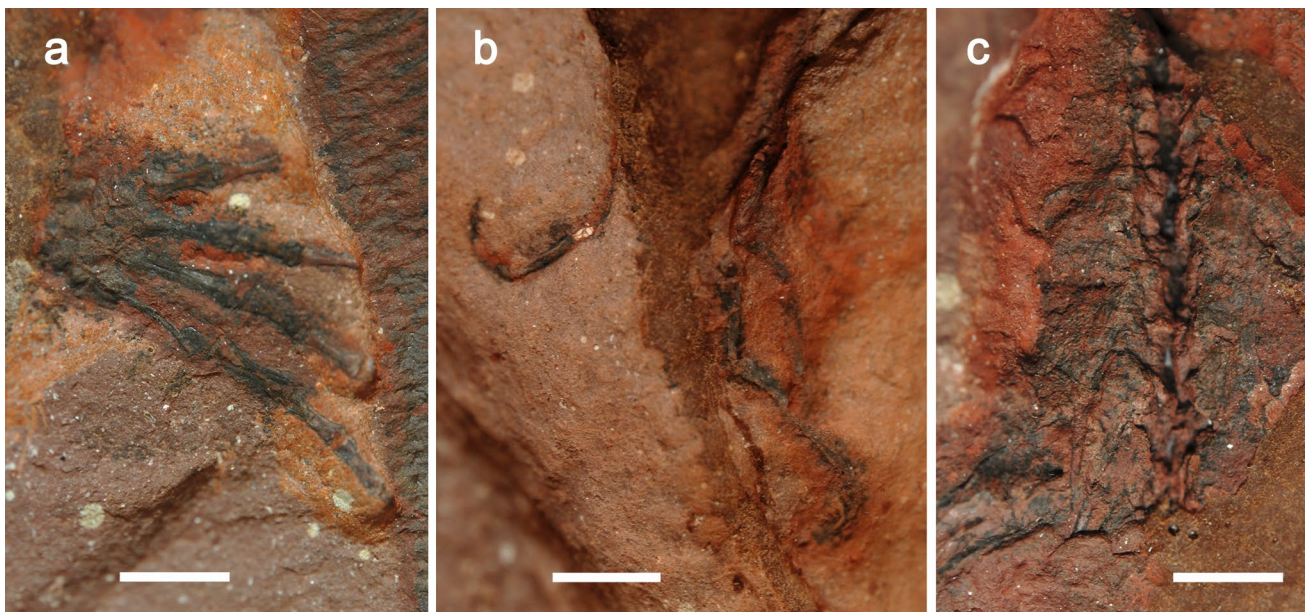


Fig. 11 Close-ups of MNC-TA0269 of *Ascendonanus nestleri* gen. et sp. nov. **a** Left manus; **b** left pes; **c** natural cast of cervical region. Scale bars measure 5 mm

The posterior portions of the articulars or prearticulars are preserved in MNC-TA0906 (Fig. 23). The articular glenoids for the quadrate condyles are visible in MNC-TA0269 (Fig. 21). There is an inconspicuous retroarticular process.

Tooth type—The dentition is more similar to derived varanopids than to basal forms, such as *Archaeovenator* and *Pyozia*, which bear stout, conical teeth. In *Ascendonanus*, slender teeth with a moderate curvature dominate, at least in the upper jaw (Fig. 27). MNC-TA0924 shows an increased degree of curvature in its caniniform region, resembling that

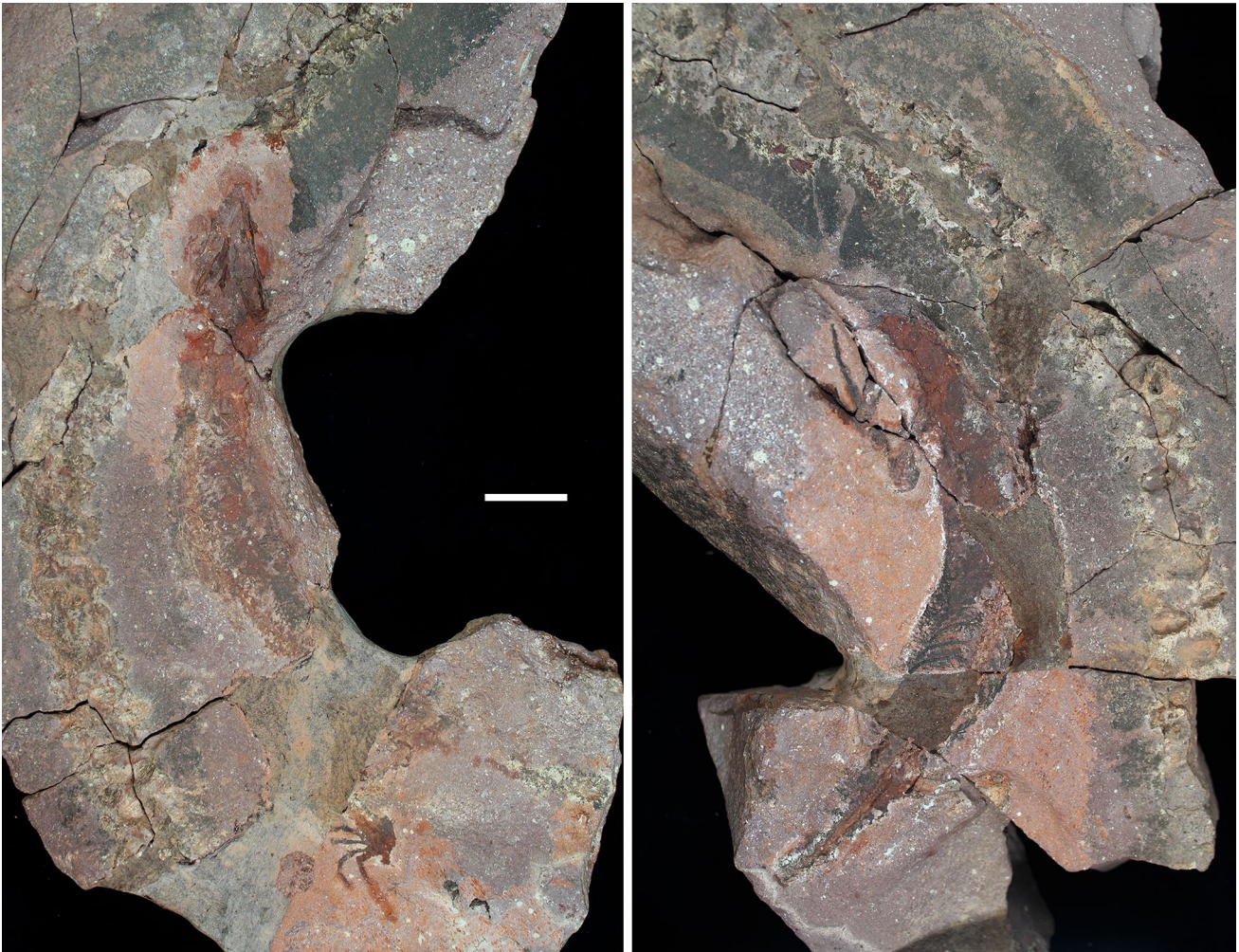


Fig. 12 Counterslabs of MNC-TA0906 of *Ascendonanus nestleri* gen. et sp. nov. On the convex side of the skeleton, the fertile tip of a twig is marked by regular pits. Scale bar measures 2 cm

of "mycterosaurines." Straight teeth dominate in the dentary of *Ascendonanus*, with weakly bulbous tips visible in MNC-TA0906. There is no trace of flattened cross sections, a cutting edge or serration.

Visceral skeleton—Only vague evidence for the stapes can be used. If correctly identified in MNC-TA0147 and TA0906, the quadrate process is elongated, as is in *Mycterosaurus* (Berman and Reisz 1982), but not in *Mesenosaurus* and *Varanops* (Reisz and Berman 2001: fig. 3b and Brinkman and Eberth 1983: fig. 8b, respectively).

Hyoids might be present in the skull of MNC-TA0906 (Fig. 23). The alternative interpretation of the two rod-like elements would refer to the ventral edge of the pterygoid quadrate processes. It seems unlikely that both pterygoid rami are exposed in an exact ventral aspect with a sub-rectangular outline, while being separated from the quadrates, which are apparently in place. Therefore, these elements are most likely hyoids. They closely resemble the arrangement

as observed in *Pyozia* (Anderson and Reisz 2004: fig. 1). In contrast to all previously known varanopids, the hyoids of *Ascendonanus* do not project beyond the skull (Online Resource 3: character 104).

Postcranial axial skeleton. The number of presacral vertebrae is outstandingly high. Graphical completion of skeletal documentations leads to an estimation of 34 in MNC-TA0269 (Fig. 20; without the atlas, if the first preserved is the axis) and 37 presacrals in TA1045 (Fig. 24; without the atlas). The appearance of a shorter trunk in MNC-TA0924 (Fig. 16) results from the uneven bedding with an up-arching trunk portion. Judged from the anterior position of the shoulder girdle and the observation that the neck is approximately as long as the skull, as in other small varanopids, the elongation is assumed to relate to the trunk portion. Such a high number strongly contrasts with the number of 26 in most other Paleozoic synapsids and early amniotes in

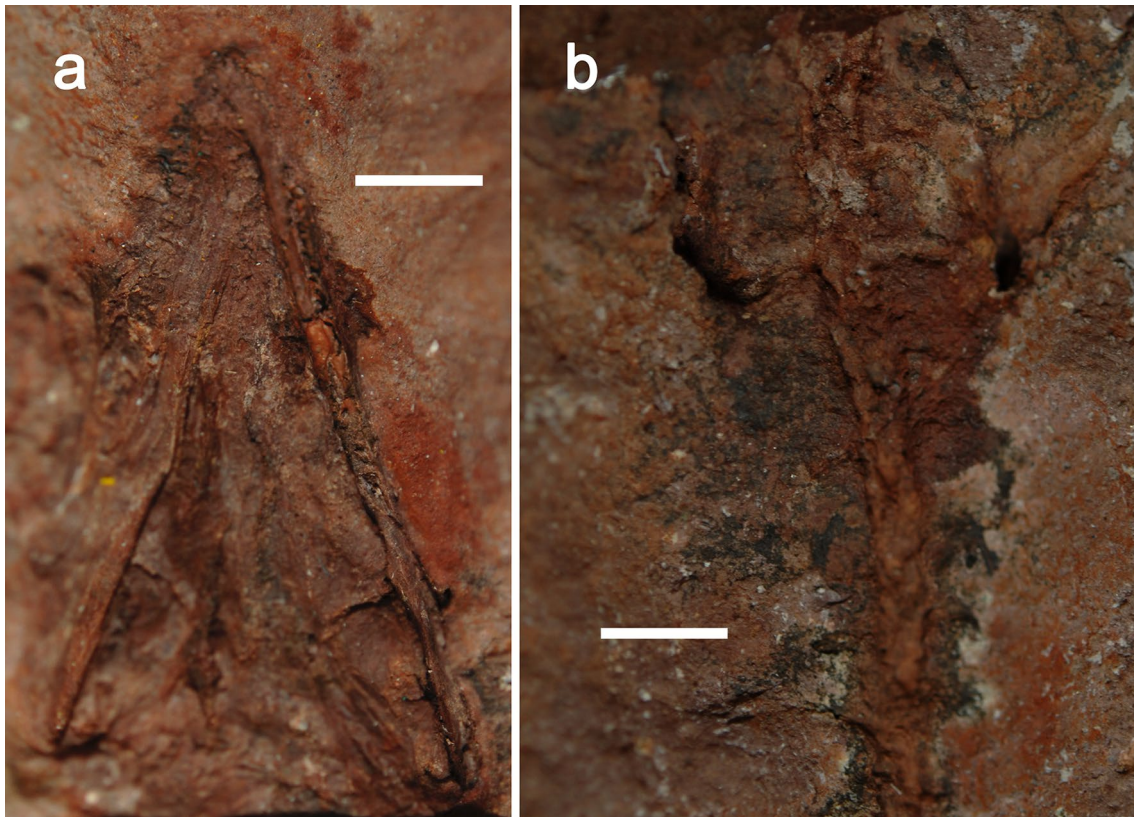


Fig. 13 Close-ups of MNC-TA0906 of *Ascendonanus nestleri* gen. et sp. nov. **a** Skull in ventral exposure; **b** natural cast of hip region. Scale bars measure 5 mm

general. Müller et al. (2010) found a generic constitution to be the reason for limited plasticity of vertebra numbers in synapsids, while reptiles are capable of easier evolutionary changes. Given that basal Caseasauria confirm the plesiomorphic amniote condition (Spindler et al. 2016) and that no early amniotes except saurian diapsids or the aquatic mesosaurian parareptiles distinctly differ from this plesiomorphy, the increased total number of presacrals in *Ascendonanus* appears to be highly adaptive. A strong selective factor related to the trunk movement caused this unique condition in *Ascendonanus*.

MNC-TA0924 exhibits an articulated atlas-axis complex (Figs. 17, 28), containing a seemingly small atlas. The axis spine is low, as in other small varanopids, and longitudinally expanded. More posteriorly, MNC-TA0906 exposes shorter, distally broadened ribs that mark the cervical-dorsal transition around the level of the glenoid region. Using rib intervals as a measure, the cervical vertebrae are not longer than the dorsals.

Anterior dorsal centra are bluntly ridged on their ventral side of MNC-TA0147. A tracing of the notochordal canal is possible in MNC-TA0269. All preserved dorsal spines are consistently low rectangular in lateral aspect. No indication for inclined lumbar spines was recognized. On the lateral

surface, the neural arches are unexcavated, which is typical for most of the smaller varanopids. The diapophyses are short and the postzygapophyses widely spaced.

There are two sacrals, indicated by their rib assignment. Of the caudal sequence, only the anterior portion is known, whereas the middle to distal parts are covered with scutes. All proximal spines are short, longitudinally less expanded than in the dorsal section.

The dorsal ribs are slender and moderately curved along their entire shaft. In the posterior sequence, they decrease in length. The rib heads appear holocephalous (Fig. 28b), as described from several small varanopids (Reisz and Dilkes 2003; Botha-Brink and Modesto 2009; Modesto et al. 2011), therefore introduced as a new character (Online Resource 3: character 119).

The first sacral rib is enlarged on both its terminal regions. The second is slender and misses contact with the first one distally. This inequality in sacral rib dimensions is probably plesiomorphic within a synapsid context, but shared only with some varanodontine varanopids, whereas *Archaeovenator* and several derived varanopids bear a first sacral rib, which equals the size of the posterior ones. Large, hook-like caudal ribs are present at least to the fifth position.



Fig. 14 Counterslabs of MNC-TA1045 of *Ascendonanus nestleri* gen. et sp. nov. Scale bar measures 2 cm

Appendicular skeleton. Pectoral girdle—Several clavicles are preserved, exposing their slender ventral plates. No cleithrum could be identified.

The interclavicle head bears a massive anterior process, similar to the plate-like condition in *Archaeovenator*, *Apsisaurus* and *Varanops*, which contrasts with the T-shaped outline seen in *Limnoscelis*, several reptiles, *Oedaleops*, *Pyozia* and *Aerosaurus* (Online Resource 3: character 124). Posterolaterally, the interclavicle is webbed between the transverse process and the shaft, not as angled as in *Pyozia* and Varanodontines. *Archaeovenator* and *Apsisaurus* show

pointed lateral spikes originating from the transverse bars of the interclavicular head, also shared with *Oedaleops* and *Echinerpeton* (Online Resource 3: character 126), but lacking in *Pyozia*, *Ascendonanus*, as well as all the few known interclavicles of derived varanopids.

Due to its orientation within the body relative to the compaction, no scapula is exposed. Of the coracoid, nothing can be described but the absence of a pronounced triceps process, which contrasts with *Archaeovenator* and certain varanodontines.

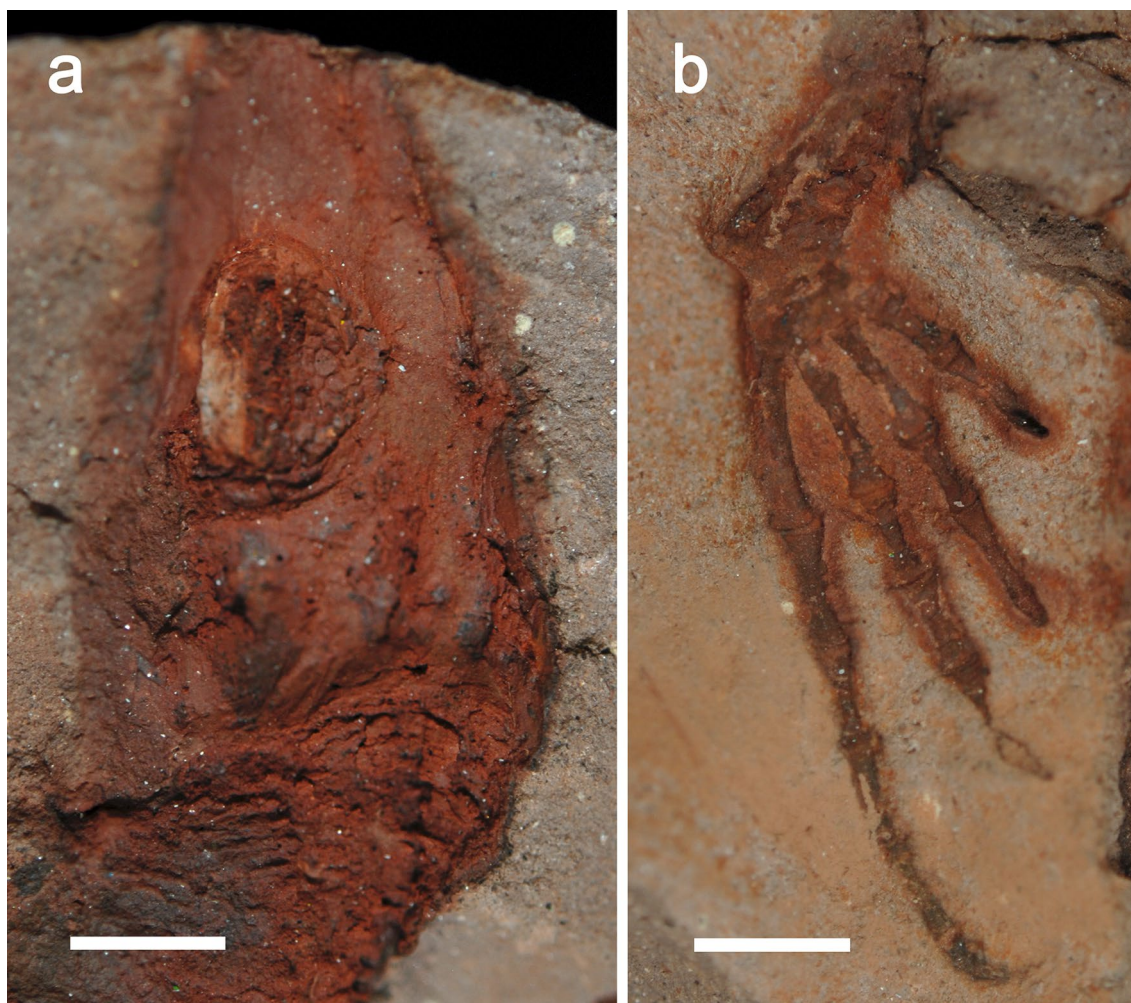


Fig. 15 Close-ups of MNC-TA1045 of *Ascendonanus nestleri* gen. et sp. nov. **a** Interior aspect of skull table; **b** left manus. Scale bars measure 5 mm

Pelvic girdle (Fig. 28)—The iliac dorsal process is low, but taller at the level of the acetabulum than that of basal reptiles and ophiacodontids. Its slightly emerging blade with a small anterior process is typical of all varanopids (Online Resource 3: character 135) and distinct from the taller blades of sphenacomorphs and caseosaurs, apart from the very similar iliac blade of *Eocasea* (Reisz and Fröbisch 2014: figs. 1, 3). No dorsal trough could be identified. The ventral part of the pelvis does not expose any informative feature but the absence of a pronounced pubic tubercle.

Limb proportions and long bones—Mainly due to the trunk elongation, the hindlimbs are significantly shorter than the trunk, which is shared with all non-“mycterosaurine” varanopids. The forelimbs are nearly as long as the hindlimbs, also reflected by the length ratio of the stylopods.

Only limited information can be given on the humerus. The distal portion is slender, as in other non-varanodontine varanopids. Even the entepicondylus is reduced, which

is shared only with *Apsisaurus* (Laurin 1991), SAM-PK-K8305 (Botha-Brink and Modesto 2009) and some early parareptiles. Another rare feature is the presence of an ectepicondylar foramen next to the supinator process of MNC-TA0924 (Fig. 16), otherwise observed in only one varanopid (Botha-Brink and Modesto 2009). In accordance with some other varanopids, the olecranon of the ulna is reduced in size.

The femur of *Ascendonanus* is slender, which is typical of smaller varanopids. The poor preservation of bones hampers additional observation of details. In the distal femur, the articular surface cannot be reconstructed regarding the relative position of the condyles. MNC-TA0906 seems to indicate the proximal edge of the internal trochanter tracing through the compressed bone (Fig. 28d).

Autopodia—Articulated feet allow for some detailed observations on carpals, tarsals and metapodia (Fig. 29).

The manual intermedium is slender. The radiale is relatively small when compared to some early reptiles or varanodontines. In contrast to most varanopids, the ulnare is more slender. No conspicuous pisiforme was identified. Both manual centrals are of about the same dimensions. As in most other varanopids, the fourth metacarpal is longer than 45% of the radius length, used as a measure for the manus length. The fifth metacarpal is significantly shorter than the fourth, which is a characteristic feature of varanopids, although not testable in some early reptiles. As a rare condition in early synapsids, no proximally overlapping metapodials were observed in the articulated autopodia.

The pes is elongated as in other small varanopids. Like in *Mycterosaurus*, the perforating foramen tunneling between the proximal tarsals is only visible as a notch in the astragalus. The astragalus neck is low, as in most varanopids except for *Archaeovenator* and *Ruthiromia*. The first metatarsal is not as shortened as in derived varanopids. A potential autapomorphy is seen in the third metatarsal, being only slightly shorter than the fourth, in contrast to the greater proportional difference seen in other varanopids.

Little is known on the phalanges of non-varanodontine varanopids. They are slender in most other representatives, contrasting with the broad phalanges of *Mesenosaurus*, resembling diadectomorphs, derived caseids and ophiacodontids, as well as varanodontines. *Ascendonanus* shares very slender phalanges with *Archaeovenator*, but is autapomorphic in the elongated phalanges of the fifth toe of the pes. The fifth toes of all autopodials are separated from the others by a greater angle, as they sometimes occur on a different level in the matrix rock.

All exposed ungual phalanges show an exceptional radian. *Ascendonanus* bears the strongest claw curvature ever recorded in a Paleozoic tetrapod (see Sect. 6). This contrasts with other varanopids (Maddin and Reisz 2007; pers. obs. F.S. 2015 on *Mesenosaurus*), including *Tambacarnifex* with a stronger curvature that might be autapomorphic (Berman et al. 2014). Like in most basal synapsids, the unguals of *Ascendonanus* show a pronounced flexor tubercle.

Phylogenetic Analysis of the Varanopidae

State of the art

After Romer and Price (1940) coined the paradigm 'Varanopsidae' to address a basal portion of their 'Sphenacodontia,' this concept was maintained even until the cladistic age (Reisz 1980). Since Brinkman and Eberth (1983) plotted *Varanops* and *Aerosaurus* as a sister group

to *Casea*, together forming the most primitive branch of Synapsida, a more basal position of varanopids is continuously accepted. The merged tree of Reisz (1986) then became the leading hypothesis, in which the concept of Eupelycosauria (Kemp 1982) as the sister group to Caseasauria has been supported, and 'Varanopseidae' form the basal-most branch within the Eupelycosauria. The basal synapsid interrelationships after Reisz (1986) were not questioned until Benson (2012), who stated changed positions for Caseasauria and Ophiacodontidae. Relating to the Varanopidae, this discrepancy can be reduced as follows: the node including all Caseasauria stands opposite to the node including the Varanopidae and the Ophiacodontidae, with *Ianthodon* plus Sphenacomorpha forming either the sister to Ophiacodontidae (Reisz 1986; and followers) or Caseasauria (Benson 2012; Online Resource 1: Fig. A2).

The first cladistic analysis providing a greater resolution of Varanopidae was presented by Reisz et al. (1998). All subsequent modifications (for example, Modesto et al. 2001; Reisz and Dilkes 2003; Maddin et al. 2006) and even the revised approach by Benson (2012) have developed rather clear inner systematics of basal and varanodontine varanopids. Thus, it can be expected that the phylogenetic analysis of varanopids produces a reliable hypothesis. It is consensually accepted (1) that *Archaeovenator*, *Pyozia* and *Apsisaurus* represent basal varanopids; (2) Mycterosaurinae (coined by Reisz and Berman 2001 for derived, small varanopids) form a sister taxon to Varanodontinae (Modesto et al. 2001); (3) the basalmost varanodontine clade consists of *Aerosaurus* and *Ruthiromia* (with the latter included to a cladistic analysis for the first time by Benson 2012), whereas *Watongia* and *Varanodon* as well as *Tambacarnifex* and *Varanops* are the most derived forms.

There are few uncertainties. One exists concerning *Elliotsmithia* from South Africa, which has frequently been found to be the basal-most member of the stem-based Varanodontinae (sub-family named by Reisz and Berman 2001; also claimed by Modesto et al. 2001, although not including *Elliotsmithia* after their analysis). This is contrasted by several trees that plotted *Elliotsmithia* among "Mycterosaurinae" (Modesto et al. 2001; Botha-Brink and Modesto 2009; only stratocladistics of Campione and Reisz 2010; by morpho-matrix again in Berman et al. 2014). Reisz and Modesto (2007) have shed light on the conflicting interpretations of *Elliotsmithia*.

Basal varanopids have lately been recognized (Reisz and Dilkes 2003). Reisz et al. (2010) did not even cite Anderson and Reisz (2004), whereas Benson (2012) did, but ignored Reisz et al. (2010). The first analysis that included all known basal varanopids was carried out by Brocklehurst et al. (2016).

The greatest unsteadiness concerns the "Mycterosaurinae," for which no consensus about the interior topology



◀**Fig. 16** In-situ drawing of MNC-TA0924, holotype of *Ascendonanus nestleri* gen. et sp. nov. **a** Ventral aspect of dorsal parts, indicated by hollow imprints of vertebral spines; **b** counterslab. Scale bar measures 5 cm

exists. The previous analyses also do not show any consensual grouping among *Mycterosaurus*, *Mesenosaurus*, *Heleosaurus* and *Elliotsmithia*, and a preferable polarity cannot be concluded from the literature (Online Resource 1: Fig. A2).

Regarding the newly described *Ascendonanus nestleri*, the preliminary determination had assumed a reptilian status until the second author R.W. recognized its synapsid nature. Interestingly, this confusion had applied to varanopid synapsids several times before, caused by earlier taxonomic concepts as well as an overall similarity with Paleozoic diapsids. The lacertoid bauplan of small varanopids led former workers to classify it as 'Eosuchia' and/or 'Eolacertilia,' comprising early neodiapsids to basal lepidosauromorphs. This solved issue was last addressed by Reisz and Modesto (2007), who counted *Mesenosaurus*, *Elliotsmithia*, *Heleosaurus* and *Archaeovenator* as previously mistaken genera, and Reisz et al. (2010), adding *Apsisaurus*. As a remarkable fact in addition to Reisz and Modesto (2007), *Mesenosaurus* was discussed regarding its varanopid affinities by Romer and Price (1940). Later, Watson (1957) counted *Mesenosaurus* and South African varanopids as reptiles close to Millerettidae. *Mesenosaurus* was not mentioned in the encyclopedia by Reisz (1986).

Probably, a reverse case might have happened for the type of *Lanthanolania*, which was originally labeled as *Mesenosaurus* (Modesto and Reisz 2002). Another basal neodiapsid, *Orovenator* (Reisz et al. 2011b), resembles the basal varanopid *Archaeovenator* in an apomorphic naris and septomaxilla, whereas the laterally incised parietals reveal its true affiliation.

Data set and cladistic test

For resolving the inner and outer systematics of Varanopidae, a new character list has been designed (Online Resource 3) based on all previous workers (Online Resource 1). The two major approaches of character selection are given by Benson (2012) and, on the other hand, Reisz (1986) to Berman et al. (2014), whereas Romano and Nicosia (2015) did not contribute to issues of the interrelationships of synapsid subgroups. The present revision of characters found various errors or inappropriate conditions in the published analyses.

The list of operational taxonomic units (OTU) is extended by so far unattended or rarely included forms. For example, the fragmentary Gondwanan varanopids are tested with specimen-based resolution, for which a closer explanation is given in Online Resource 3. Moreover, *Anningia* has been excluded from Varanopidae at a time

when the re-evaluation of South African representatives just started (Dilkes and Reisz 1992). From a modern point of view, it is doubtlessly a varanopid, especially since our current knowledge on juvenile therapsids does not allow for a match with *Anningia*.

There are uncertainties about postcrania assigned to the basal caseosaur *Oedaleops*. Langston (1965) described only few postcrania that he only vaguely determined as belonging to the well-preserved holotypic skull. Sumida et al. (2014) were confident to ascribe a greater amount of postcrania to *Oedaleops*. New scorings are possible for the coronoid eminence, dimensions of centra, spine shape, interclavicle, pubis, ischium and unguals. Unfortunately, the authors missed addressing some deviations from the description by Langston (1965), such as the shape of the iliac blade, the humerus (not coded herein) or the distal femur. Therefore, different lines were written for the described versions of *Oedaleops*, as well as a cranial OTU, for testing the influence of this issue.

In general, the question of the validity of Eothyrididae (Reisz et al. 2009; Sumida et al. 2014; Brocklehurst et al. 2016) is heeded by a full inclusion of relevant characters. The enigmatic early synapsid *Echinerpeton* (Reisz 1972) has rarely been included in cladistics tests before. *Milosaurus*, originally described as a varanopid (DeMar 1970), is included for the first time, but suspected to plot close to the ophiacodontid *Varanosaurus* because of limb proportions. For comments on the used OTU and their relative matrix completeness, see the introduction of Online Resource 3.

Although phylogenetic analyses are a proper way to raise hypotheses, recent literature contains some overestimation of cladistic abstraction, with inflationary production of values and alternative trees. Beyond the general issue of abstraction in living systems and incompleteness in fossil morphology restricted to osteology, Paleozoic vertebrates are even more affected by fragmentation. Sansom et al. (2010) demonstrated that data incompleteness causes stem-ward slippage, which cannot be compensated within a system of competing minimum tree positions. Since parsimony per se as well as the use of characters despite their dependent and uncountable nature is an act of abstraction, no substantial significance is expected from further steps. This means that cladistics is used herein for an overview and to find potential synapomorphies, whereas robustness values mainly reflect the completeness and distinctness of included taxa. Taxa definitions result from morphology rather than measured values that change with any modifications of the character list or taxa list. Moreover, robustness of the resulting tree hypothesis is not comparable to former analyses, while the immense number of observations and corrections is recommended to be paid the highest attention.

One hundred seventy-seven characters were coded, with excluded characters explained in Online Resource 3. The

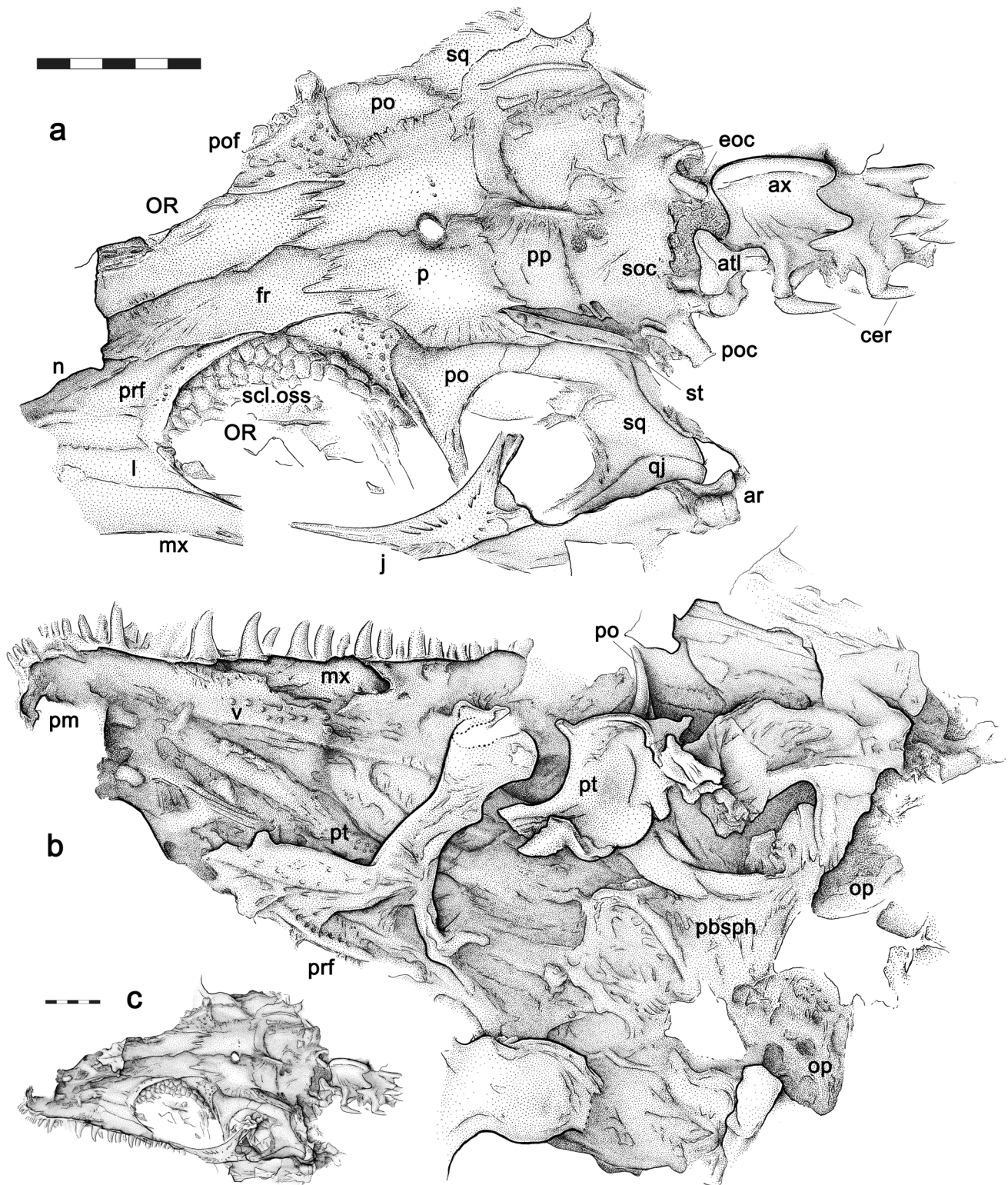


Fig. 17 Cranium and anterior cervical column of MNC-TA0924, holotype of *Ascendonanus nestleri* gen. et sp. nov., drawn from silicon casts. **a** Dorsal aspect; **b** palatal aspect; **c** combination of both, revealing the true outline of the crushed skull. Scale bar measures 5 mm

analysis was run in PAUP* 4.0b10 (Swofford 2001). Multi-state matrix entries were treated as polymorphism, corresponding to actual observations. No outgroup was defined. After trying numerous combinations, most non-synapsid OTUs were deleted because of destabilization of the tree topology. The final tree comprises 38 OTUs. The heuristic search was carried out several times, with 114 trees constantly saved. No wild-card taxa were recognized, meaning that even fragmentary OTUs can be included to a single strict consensus (unresolved portions retained in a 50% majority rule tree). Nonetheless, observations of the topologic behavior of certain OTUs during alternative combinations are used for the subsequent discussion. It is remarkable that the single strict consensus (Fig. 30) contains similarities to the independent results of Brocklehurst et al. (2016). Bootstrap resampling values after 100 replicates are indicated in Fig. 30, demonstrating an overall low support even for commonly accepted clades. This support is partially biased by serious matrix gaps resulting from fragmentary and deviant OTUs. In general, the detailed revision of characters already revealed a high potential for homoplasy affecting the tree portion in question. Whereas former analyses might have been too optimistic, several early amniote character histories are poorly understood, especially among small varanopids.

Taxonomic results

In the following discussion of cladistic interim results, apomorphies of the tree shown in Fig. 30 are included when either unambiguous or unequivocal. Where both criteria are met, this is marked. However, these criteria depend greatly on the list of included OTUs and therefore are not taken as requirements for diagnostics over differential comparisons. Character numbers appear in brackets and correspond with Online Resource 3. Caused by great matrix gaps, various character histories are questionable, making an increased future understanding of varanopid osteology rather urgent.

Outgroup

Eight non-synapsid taxa were suggested to polarize the character history of varanopids: two basal Diadectomorpha (*Limnoscelis*, *Tseajia*), three Eureptilia (*Paleothyris*, *Protorothyris*, *Captorhinus*) and three early Parareptilia (*Milleropsis*, *Erpetonyx*, *Australothyris*). In order not to set anticipatory constraints, no defined outgroup was used. Notably stronger than eureptilian OTU, parareptiles appeared polyphyletic, with *Australothyris* (same as for *Captorhinus*) showing affinities to Caseasauria, whereas *Milleropsis* and *Erpetonyx* plotted among basal Varanopidae. Nonetheless, this is not taken as an indication of the polyphyletic dissolution of Synapsida, since the characters of the chosen early reptiles were not fully included. Although not considering

the widely accepted monophyly of Synapsida as a given fact, it should be noted that the used data set is not suitable for investigating this question. By contrast, the behavior of potential outgroup taxa yields the informative conclusion that the symplesiomorphic compliance of early amniotes is well reported within less derived varanopids to a certain extent. The most stable tree could be found when including *Paleothyris* and *Protorothyris* as the only non-synapsid OTU. The earliest known parareptiles, *Captorhinus*, and known diadectomorphs are already more derived within their lineages, whereas basal Romeriida and Varanopidae retain basal amniote conditions the most.

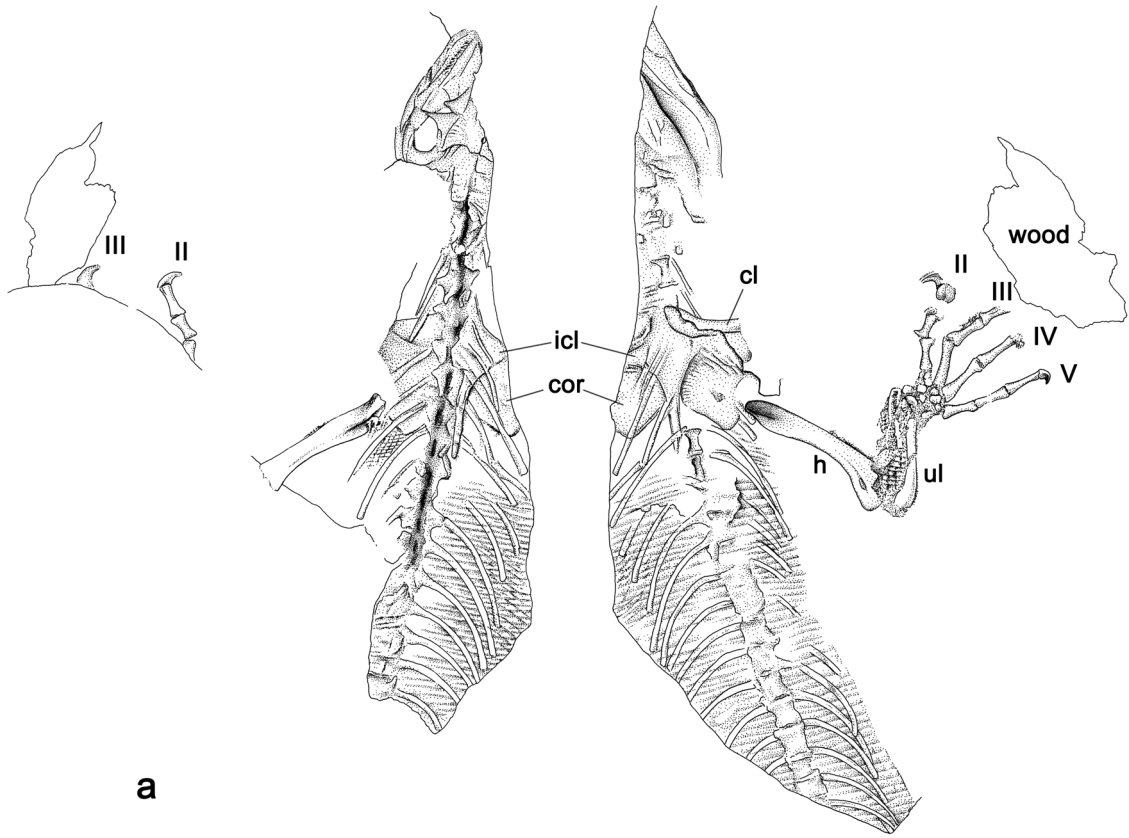
In the current combination, Synapsida can be diagnosed by the lateral temporal fenestra (7; unambiguous and unequivocal), a maximum of five precaniniform maxillary teeth (29), a laterally directed basiptyergoid processes (74), a rod-shaped stapes (103) and a posteriorly round entepicondyle (154).

Caseasauria

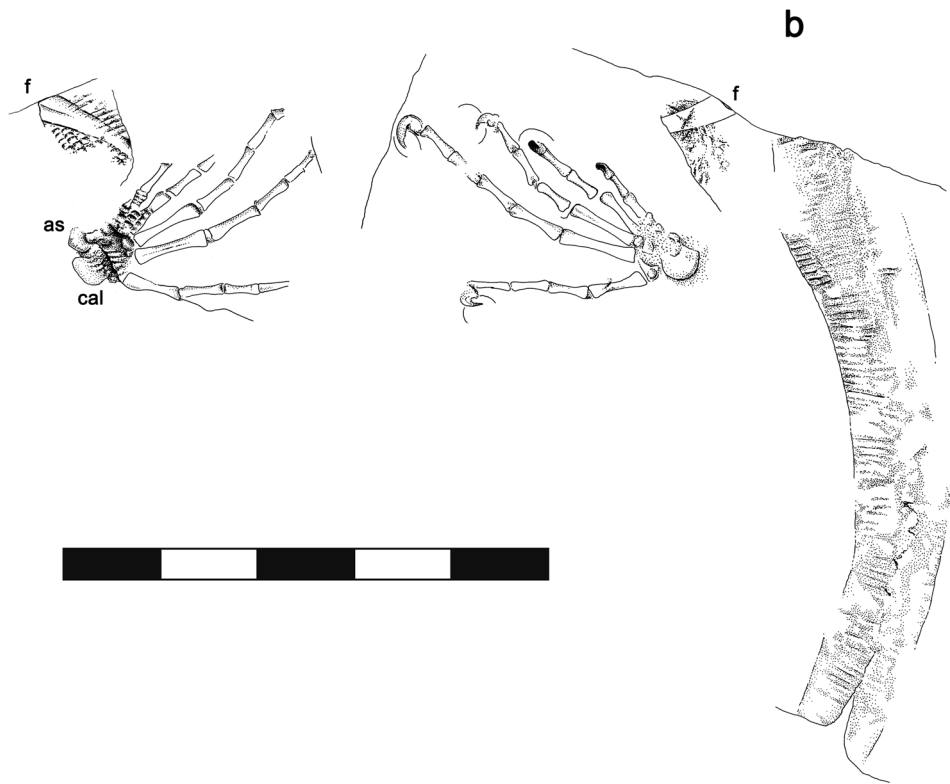
Caseasaurians are confirmed as the basalmost branch of synapsids (Reisz 1986; Brocklehurst et al. 2016), so that the concept of their higher position (Benson 2012) could be settled. Testing the present data set without reptilian polarization, the monophyletic condition of Caseasauria is lost. When including more reptiles, these sometimes plot higher than Caseasauria. Caseasaurians did not appear more derived than other synapsids in any preliminarily tested combinations. This result, shared with Brocklehurst et al. (2016), is caused by careful recoding rather than the impact of the newly identified basal caseasaurian *Vaughnictis*, since the same relationship is given when excluding this genus. In various preliminary tests, *Vaughnictis* differed slightly in its tree position, but was remarkably close to *Eothyris*.

Oedaleops was tested by the inclusion of alternative lines. It shows that there is little influence of deviant descriptions (or deletion) of postcranial characters. The knowledge of Langston (1965) equals the version based on cranial data only in a loss of resolution, under which *Vaughnictis* is depicted as unresolved next to *Eothyris* and a branch of all higher Caseasauria. In conclusion, the listed deviations from Sumida et al. (2014) can be ignored in the current state of knowledge. Moreover, the postcranial assignments by the latter authors seem applicable.

Eocasea appears as the basalmost Caseasaurian, instead of being a caseid as reconstructed by Reisz and Fröbisch (2014). This deviation could be explained by the juvenile condition of the holotype, which causes stem-ward slippage, and a more cautious coding. Nonetheless, it remains in the tree, as this oldest known caseasaurian might in fact be more basal than previously thought. The character history concerning this tree portion is ambiguous when considering



a



b

Fig. 18 In-situ drawing of MNC-TA0147 of *Ascendonanus nestleri* gen. et sp. nov. **a** Ventral aspect of dorsal parts, indicated by hollow imprints of vertebral spines; **b** counterslab. Roman numbers refer to digits. Scale bar measures 5 cm

Datheosaurus and *Callibrachion* (Spindler et al. 2016). Opposing Brocklehurst et al. (2016), the monophyletic nature of the Eothyrididae is again questionable. However, a basal caseosaurian ghost lineage pattern (Reisz and Fröbisch 2014) co-occurs with that of Varanopidae.

In the final tree (Fig. 30), Caseosauria are characterized by a contact between postorbital and supratemporal (49), a broad supratemporal (53; apparently symplesiomorphic within Amniota, but apomorphic in the two included reptiles), a posterodorsal process in the squamosal (56; shared with all smaller varanopids except *Archaeovenator*, and therefore may be a symplesiomorphy, as supported by *Tseajaia* and *Milleropsis*) and dorsal centra that lack a ventral keel (110; character history questionable). All caseosaurians that appear higher than *Eocasea* exhibit a maxilla that overhangs its tooth row (26; unknown in *Eocasea*), a narial shelf on the nasal (36; unknown in *Eocasea*) and a large pineal foramen (52; character history questionable).

In contrast to Brocklehurst et al. (2016), the recently diagnosed *Vaughnictis* appears closer to *Oedaleops* than to *Eothyris*. This supposed monophyly is based on a long postorbital-squamosal contact (48) and even femoral condyles (169; unknown in *Eothyris*, probably plesiomorphic in caseosaurians, as implied by the recent re-description of *Phreatopasma*, Brocklehurst and Fröbisch 2017). Within the given context, *Vaughnictis* and *Eothyris* share the rare apomorphy of a flat occipital slope (12), which could indeed be related to more soft tissue similarities than the counted synapomorphy with *Oedaleops*. As a result, *Vaughnictis* should still be considered a possible sister taxon to *Eothyris*, all the more since they share a similar shape of the temporal fenestra (Brocklehurst et al. 2016; character 240 was excluded because of redundancy with their character 7).

Because of a paraphyletic conception of eothyridids, the definition of Caseidae is raised as another question. In accordance with Brocklehurst et al. (2016), *Datheosaurus* and *Callibrachion* appear to form a clade. This is based on long hindlimbs (143) and probably the presence of an ectepicondylar foramen in their humeri (157). Together with *Casea* as a representative of derived caseids, a wider clade is formed on the basis of a maxillary ascending lobe (22), a concavity in the posterolateral scapula (127; unknown in eothyridids except for *Oedaleops*), and a distally broad humerus (155; unknown in eothyridids except for *Oedaleops*). Comparing these steps with caseid diagnoses, it is recommended to count *Datheosaurus* und *Callibrachion* as members of the Caseidae even under a paraphyletic

perception of eothyridid-grade caseosaurians and a stemward shift of *Eocasea*.

Eupelycosauria

The clade Eupelycosauria is confirmed as valid because of the above comments on the position of Caseosauria as their sister taxon. The definition of Eupelycosauria since Reisz (1986) has gained support by Brocklehurst et al. (2016) before. From the presented tree (Fig. 30), the characteristics of Eupelycosauria are a tall snout (4; unambiguous and unequivocal), an exposed septomaxilla (18), the initial condition of only slightly enlarged canines (31), a parietal that markedly overlaps the interorbital Sect. (50), the presence of a retroarticular process (98; character history questionable) and a considerable curvature of marginal teeth (99).

There is a stable internal node that occurs in almost all basal synapsid analyses, including Ophiacodontidae, Edaphosauridae, and Sphenacodontia. Using cladistic methods, only a single analysis has debated this clade (Benson 2012), whereas even a grouping of Varanopidae with Caseosauria (Brinkman and Eberth 1983; Sidor 1996) reflects the direct relationship of Ophiacodontidae and Sphenacomorpha. Their clade is herein named Metopophora (referring to the postfrontal brow shield). Since no basal form could be identified, it is left to future discoveries whether to use this sister to Varanopidae as a stem- or a node-based taxon. Metopophora are characterized by the following character conditions: loss of skull ornamentation (13), shield-like expansion of the postfrontal (43), broad anterior terminus on the jugal (44), a large squamosal shield (55), fused postparietals (66; character history ambiguous), loss of parasphenoid dentition (76), prominent angular ventral keel (91; unambiguous and unequivocal), tall axis spine (106), longer diapophyses (117), hind limb elongation (143) and a single deltopectoral crest (150; unambiguous and unequivocal). Some of these apomorphies resemble those of derived caseids by parallelism.

The herein used representative of Sphenacodontia is '*Haptodus*' *garnettensis*, of which a complete revision is provided in Spindler (2015; currently prepared). The contemporary *Ianthasaurus* is included as a doubtless edaphosaurid. Sphenacomorpha (Edaphosauridae plus Sphenacodontia) form a stable group. Since *Ianthodon* was found to be more basal than this node (Benson 2012; Brocklehurst et al. 2016), a stem-based definition of a wider clade is appropriate. This has preliminarily been explained by Spindler (2015) and is introduced here as Haptodontiformes. The diagnosis of Sphenacomorpha is incomplete because of the restricted taxon inclusion, but contains an increased number of precaniniform teeth (29), a twisted prearticular (96) and well-excavated neural arches (116). The wider Haptodontiformes, including *Ianthodon* and Sphenacomorpha,

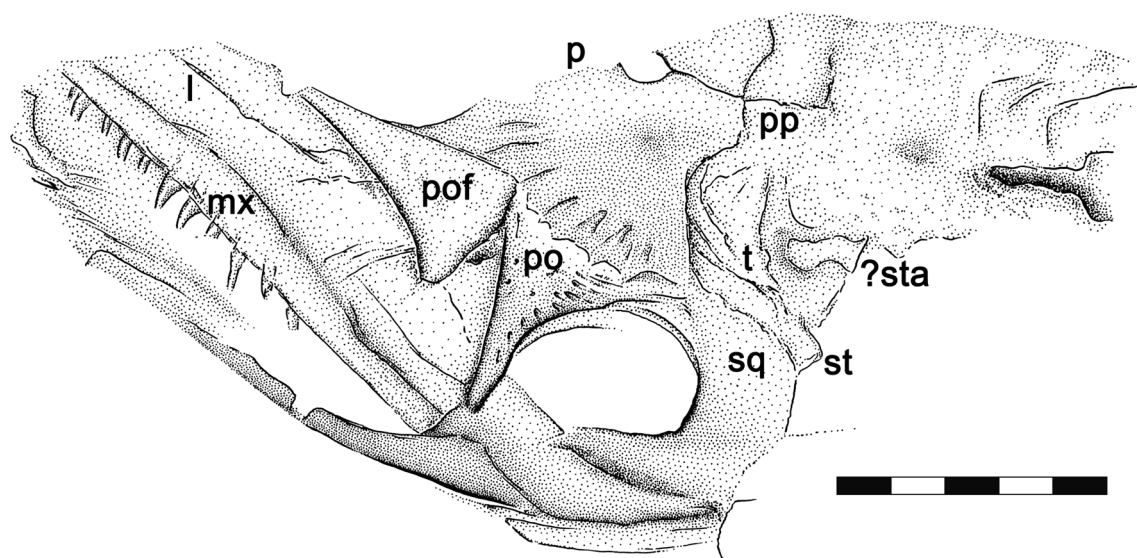


Fig. 19 Cranium of MNC-TA0147 of *Ascendonanus nestleri* gen. et sp. nov., drawn from original specimen. Scale bar measures 5 mm

count a ventrally concave zygomatic arc (10; unambiguous and unequivocal), a narrow posterior bar on the postorbital (46), loss of the quadratojugal anterior ramus (60; unambiguous and unequivocal), anteriorly directed basiptyergoid processes (74), a deeper mandible (85) and the presence of neural arch excavations (115).

Ophiacodontidae

Ophiacodontidae are treated as the stem-based sister to Haptodontiformes within Metopophora. Several forms occurred in the Pennsylvanian, with the lineage of *Varanosaurus* now dated back by its sister taxon *Milosaurus*. That Ophiacodon represents a separate lineage is confirmed by the observation that the undescribed Garnett form seems intermediate between *Archaeothyris* and *Ophiacodon* (pers. obs. F.S. 2013).

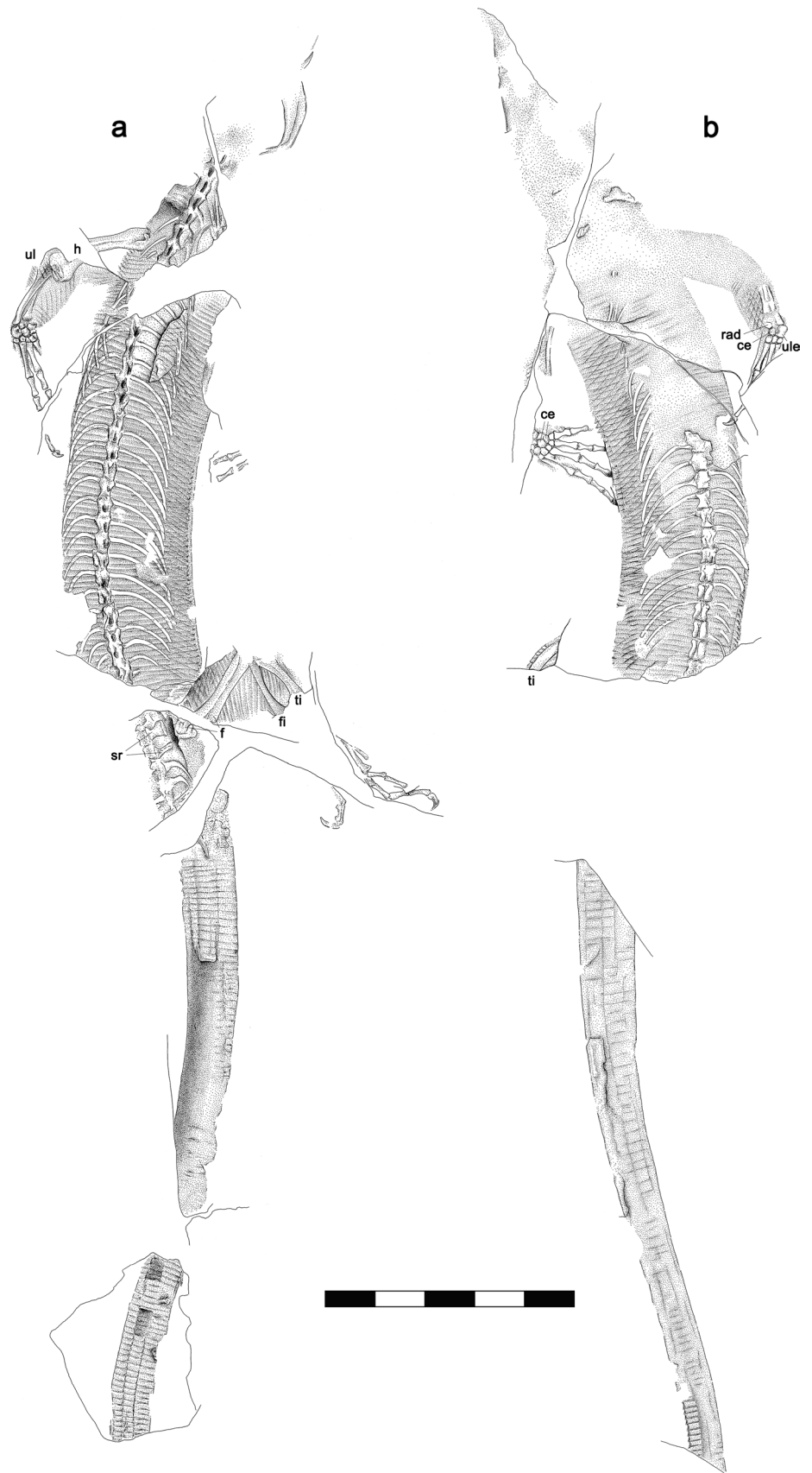
Ophiacodontidae can be diagnosed by an inclined occipital slope (12), the presence of a (shallow) maxillary dorsal lobe (21), a medial supra canine buttress (25; unambiguous and unequivocal); lateral mandibular fenestra (86; unambiguous and unequivocal) and a pronounced pubic tubercle (138). The node excluding *Archaeothyris* exhibits elongated snouts, coded via elongated nasals (35), maxilla reaching to the quadratojugal (62), medially expanded tabular to contact the supratemporal (63), reduced palatine dentition (68), small, ventrally directed basiptyergoid processes (75), a freely ending paroccipital process (83), deep fossa in the dorsal ilium (136) and a femur that is more than 120% as long as the humerus (145), all of which are unclear in *Archaeothyris*.

The rather high position for the fragmentarily known *Echinerpeton* (Fig. 30) is surprising as it dates back the radiation of Ophiacodontidae. *Echinerpeton* meets *Varanosaurus* in its deviation from the common shape of neural spines (Reisz 1972; Sumida 1989). Benson (2012) could not resolve a stable position for *Echinerpeton*, with reconstructing a position as the basal-most eupelycosaur in one test. Our own preliminary tests have shown a strong affinity to its contemporary *Archaeothyris*. Brocklehurst et al. (2016) then demonstrated that *Echinerpeton* might plot more basally than *Ianthodon* or within Ophiacodontidae. The herein presented hypothesis suggests that *Echinerpeton* is basal to the lineage of *Varanosaurus*. The character histories of both suggested apomorphies of this subclade are questionable, as they might be affected by parallelism between *Ophiacodon* and Haptodontiformes: low anterior pterygoid (71) and low axis spine (106). In contrast, the close relationship of *Varanosaurus* and *Milosaurus* is well supported by short dorsal diapophyses (117) and the long astragalus neck (175).

Varanopidae

The monophyletic status of this synapsid subgroup is well supported. Suggested synapomorphies for Varanopidae in general include a narrow zygomatic arc (8; also found in *Oedaleops*, thus possibly a synapomorphy of Synapsida according to Sumida et al. 2014: figs. 2, 13), loss of the double canine condition (32), a narrow occipital contribution by the squamosal (59; unambiguous and unequivocal), low anterior pterygoid (71), anterodorsal inclination of posterior dorsal spines (112), supraglenoid foramen anterior to buttress (129; unambiguous and unequivocal) and a metacarpal

Fig. 20 In-situ drawing of MNC-TA0269 of *Ascendonanus nestleri* gen. et sp. nov. **a** Ventral aspect of dorsal parts, indicated by hollow imprints of vertebral spines; **b** counterslab. Scale bar measures 5 cm



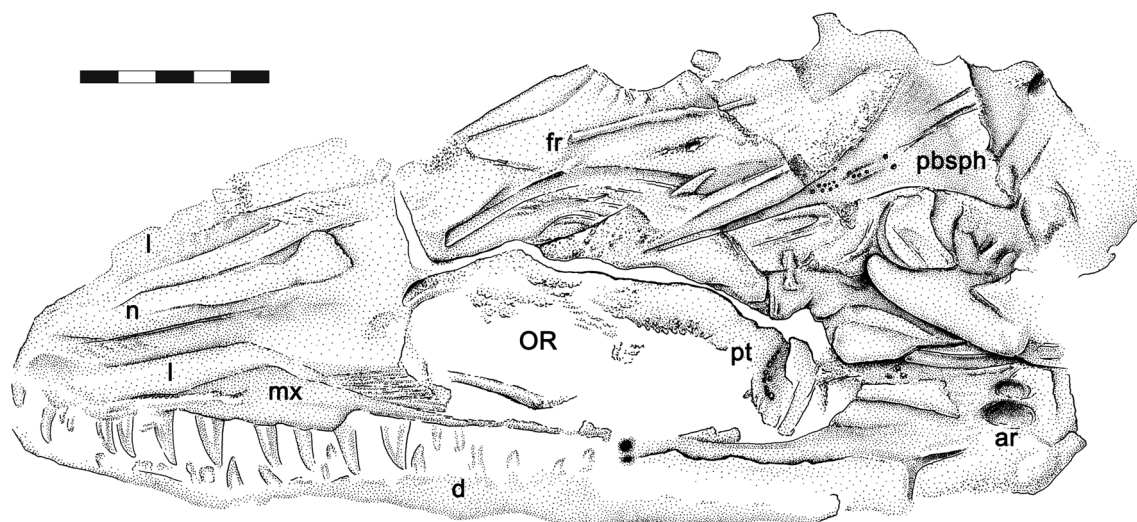


Fig. 21 Cranium of MNC-TA0269 of *Ascendonanus nestleri* gen. et sp. nov., drawn from original specimen. Scale bar measures 5 mm

V that measures not more than 60% the length of metacarpal IV (166).

Basal varanopids are rarely known, represented by three specimens known previously to the five added by the present description. The phylogenetic position of *Ascendonanus* was reconstructed as basal varanopid throughout all preliminary tests and combinations. In the final tree (Fig. 30), *Ascendonanus* does not appear as an isolated branch within a basal varanopid paraphyly, but as the sister to *Apsisaurus*, with which it may form the basal-most varanopid branch. The synapomorphies of this supposed subclade are a reduced entepicondyle (1) and reduced olecranon (159), both affected by questionable character histories due to matrix gaps. Therefore, although among the best-known varanopids, *Ascendonanus* cannot be compared to its less preserved relatives with certainty. For a full differential diagnosis, see Sect. 4 (Systematic Paleontology). Under the present hypothesis, *Ascendonanus* exhibits two stronger autapomorphies, counting subequal extremity lengths (144) and an ectepicondylar foramen (157). *Apsisaurus* can be distinguished from it by elongated cervicals (107), weakly excavated dorsal neural arches (115), and spikey lateral processes on the interclavicle (126; character history unclear, as commented on in Online Resource 3).

Regardless of a possible higher position of *Ascendonanus* or *Apsisaurus* (Reisz et al. 2010; Brocklehurst et al. 2016), *Archaeovenator* is grouped with higher varanopids by the apomorphies of an enlarged external naris (6), postorbital contact with the supratemporal (49; character history questionable), long hyoids (104) and the loss of a supraglenoid foramen (128; highly problematic, since the foramen occurs in varanodontines and *Apsisaurus*; see also character 129 used as a varanopid synapomorphy). *Archaeovenator* itself is interesting in its strong affinities with other primitive

amniotes, whereas isolated traits seem to prepare the osteology of varanodontines. One explanation could be that deep homologies occurred that were not realized in “mycterosaurine” phenotypes or that the latter had returned to certain plesiomorphic conditions of their genotypes. An alternative interpretation could be that the only known and holotypic specimen of *Archaeovenator* represents a juvenile varanodontine. Although this would be surprising in this oldest known varanopid, it could bring the argument of stem-ward slippage into consideration. It is remarkable, though, how highly autapomorphic *Archaeovenator* is: lack of skull ornamentation (13; relevant only in case of more basal positions of ornamented varanopids), absence of a frontal lateral lappet (41; juvenile condition?), a narrow posterior process on the postorbital (46), broad supratemporal (53; most likely a kept plesiomorphy), absence of parasphenoid dentition (76), spikey lateral processes on the interclavicle (126; character history unclear, as commented on in Online Resource 3), pronounced triceps process on the coracoid (134; character history questionable), lack of an initial iliac blade (135; most likely plesiomorphic, as the blade evolved independently in Caseasauria, Haptodontiformes and Varanopidae) and a long astragalus neck (175).

In accordance with most former workers, *Pyozia* could be confirmed as holding a basal varanodontid position. A more derived grouping with *Mesenosaurus* has been reconstructed by Brocklehurst et al. (2016), as well as occasionally appearing in own preliminary tests. Since both genera are from the same spatiotemporal setting, it might be no coincidental grouping. Moreover, the fragmentary nature of the holotypic skeleton of *Pyozia* could have only caused a minimal tree position, while probably representing a “mycterosaurine.” Exclusive resemblance with *Mesenosaurus* could be seen in the pterygoid

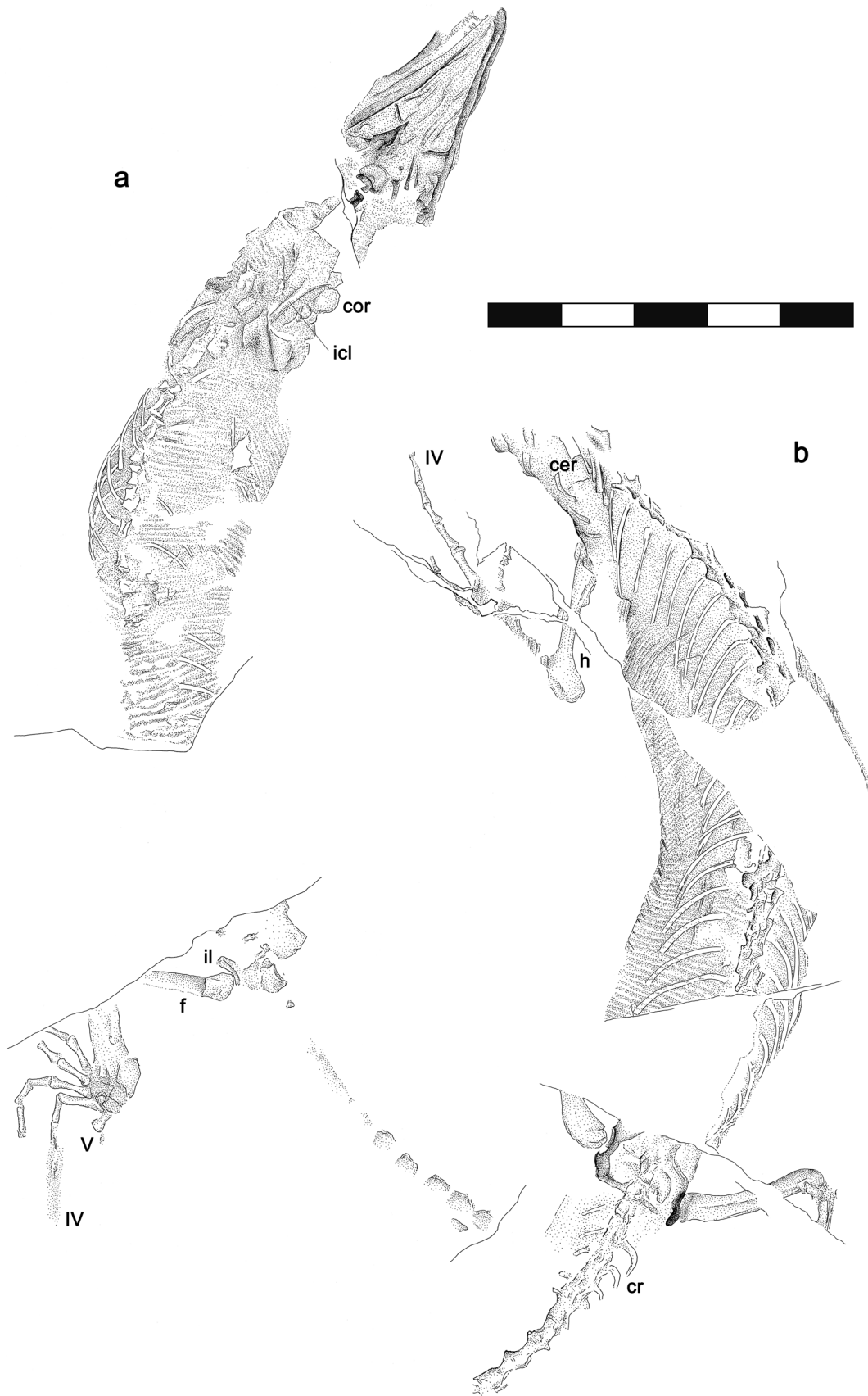
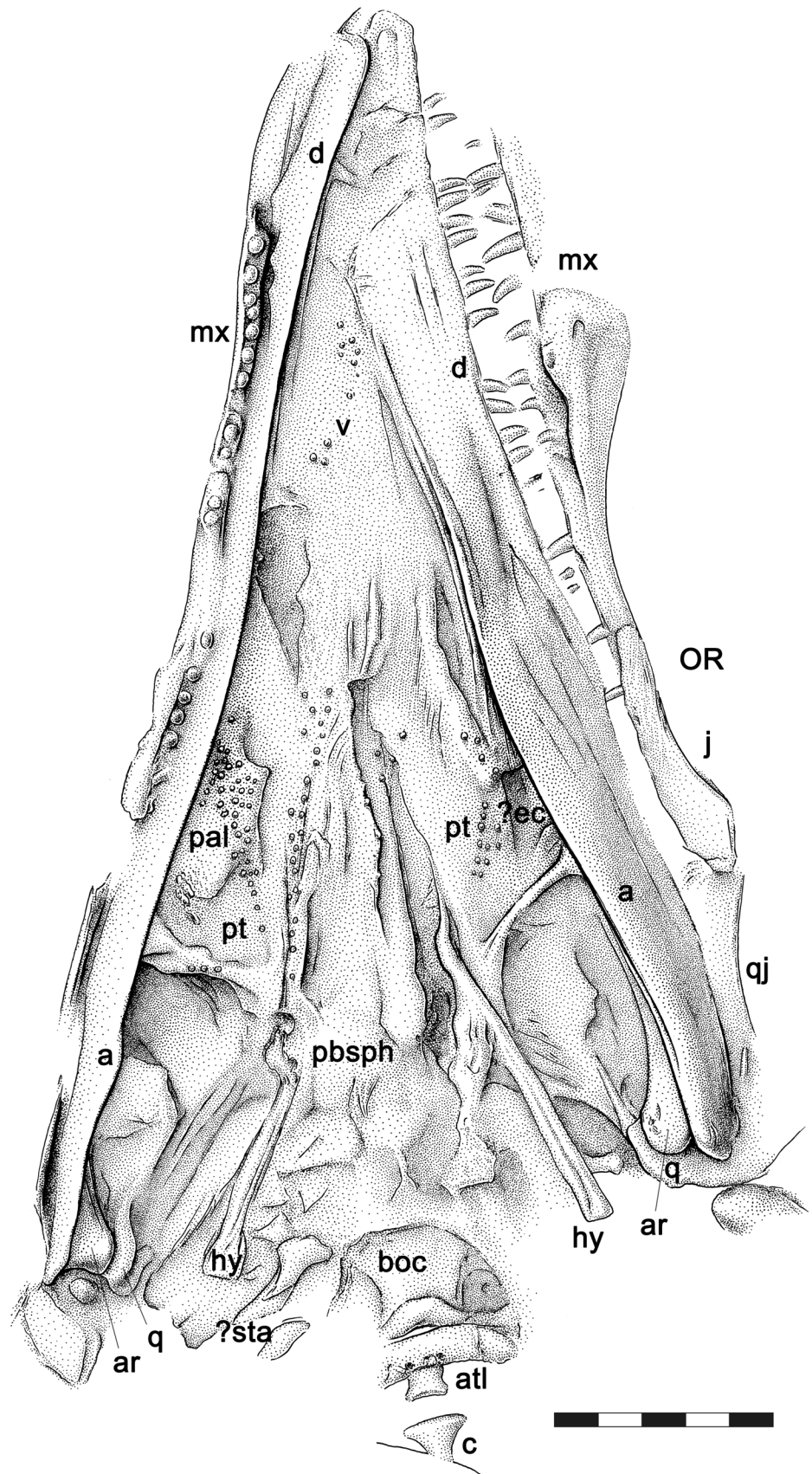


Fig. 22 In-situ drawing of MNC-TA0906 of *Ascendonanus nestleri* gen. et sp. nov. **a** Dorsal aspect on ventral parts; **b** counterslab. Scale bar measures 5 cm

Fig. 23 Cranium of MNC-TA0906 of *Ascendonanus nestleri* gen. et sp. nov., drawn from a silicon cast. Scale bar measures 5 mm



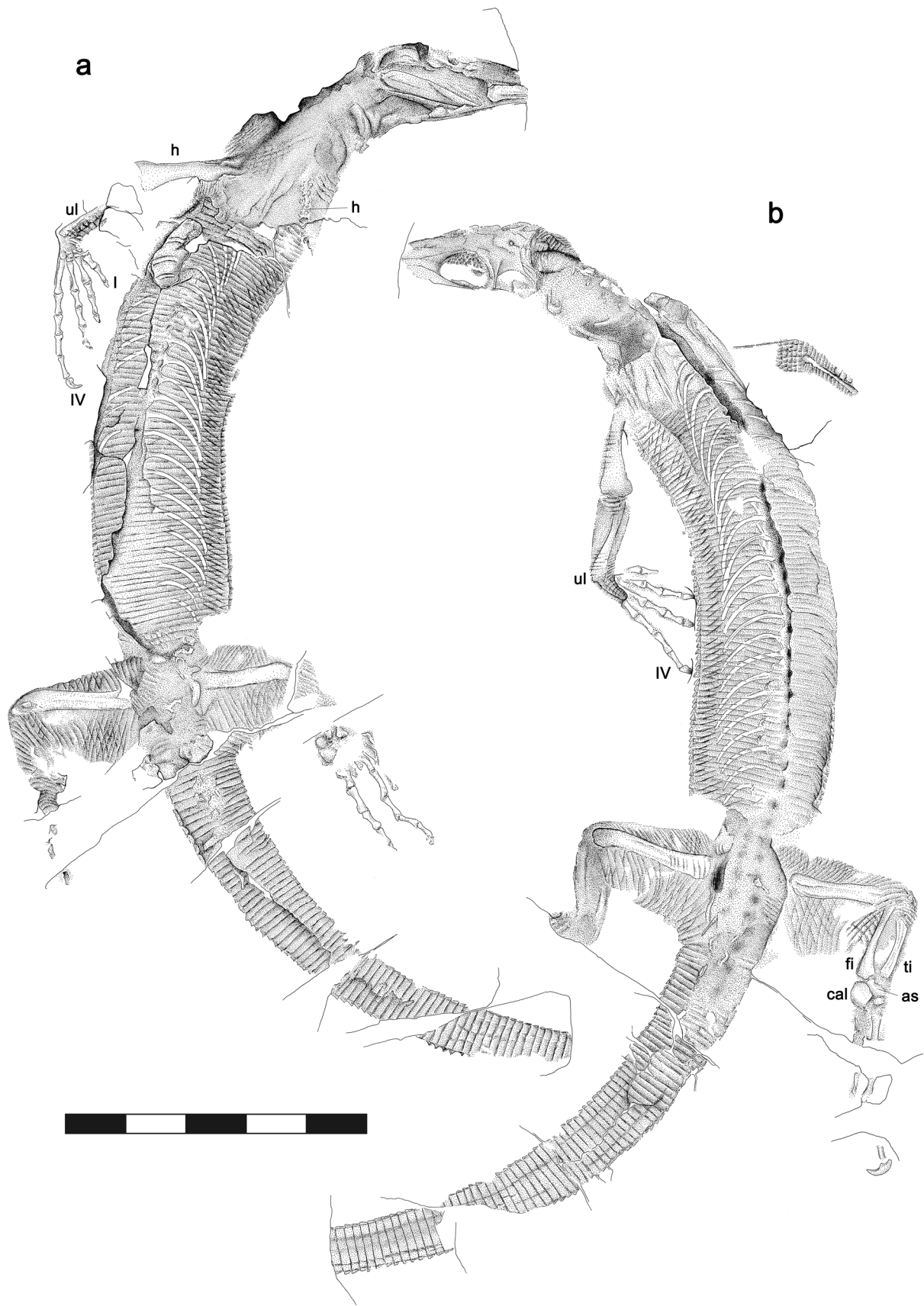


Fig. 24 In-situ drawing of MNC-TA1045 of *Ascendonanus nestleri* gen. et sp. nov. **a** Dorsal aspect on ventral parts; **b** counterslab. Scale bar measures 5 cm

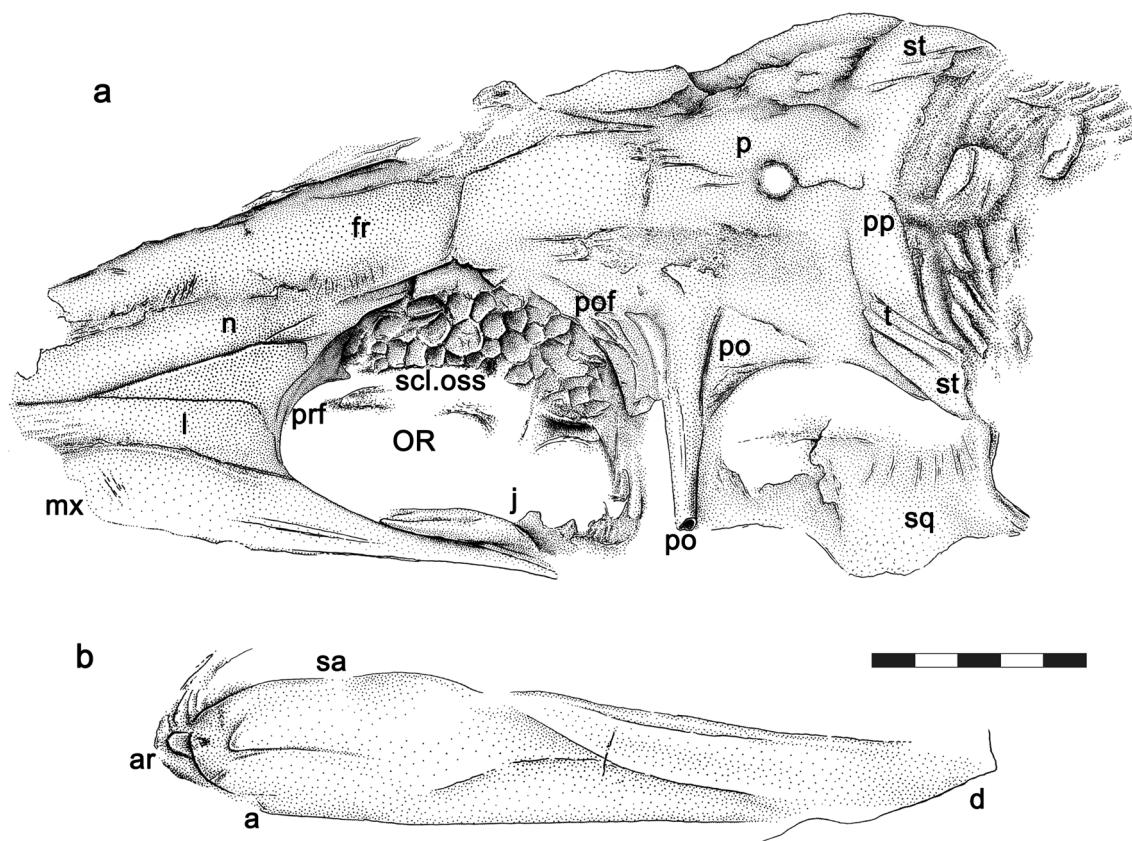


Fig. 25 Cranium of MNC-TA1045 of *Ascendonanus nestleri* gen. et sp. nov., drawn from original specimen. **a** Skull table from reversed preservation (interior aspect); **b** mandible, assumed to expose the lateral side. Scale bar measures 5 mm

transverse flange dentition (69) of *Pyozia*, but this lacks a background of doubtless character history or commonly observable preservation. *Pyozia* can be excluded from derived varanopids because of the absence of caniniform teeth, a trait shared with *Archaeovenator* (30), as well as the below-offered diagnosis of derived varanopids. With respect to canine evolution, the history of the used character definitions is problematic. Single canines within a group of indistinctly enlarged maxillary teeth are a characteristic of *Ascendonanus* and derived varanopids, somewhat intermediate between *Limnoscelis* and the single-canine pattern of Therapsida.

Pyozia can be grouped with “mycterosaurines” and varanodontines on the basis of a trapezoidal outline of the parasphenoid plate (78) and a ridge on its ventral surface (79). If both conditions show interdependencies, the grouping might appear as overrated. Again, the certain interrelationships of basal varanopids are not yet fully resolved. *Pyozia* appears autapomorphic in a reduced number of premaxillary teeth (17) and anteriorly directed basicranial processus, as in eureptiles and haptodontiforms (74). The differential diagnosis offered by Anderson and Reisz (2004) supports a basal varanopid position.

Derived Varanopidae

The sister taxon relationship of the derived varanopid subclades “Mycterosaurinae” and Varanodontinae is well reported in all published analyses. Therefore, this robust node-based taxon is introduced as Neovaransia in this study. Its diagnosis includes a paroccipital process that extends far laterally (82), strongly curved teeth (100) and compressed teeth to form cutting edges (101; unambiguous and unequivocal).

“Mycterosaurinae”

As demonstrated since the first introductions of this clade (Reisz and Berman 2001; paralleled by Modesto et al. 2001), lightly built derived varanopids are grouped also in the present analysis. In contrast with earlier definitions, *Mycterosaurus* is excluded from them on the basis of strong affinities to Varanodontinae. In consequence, the term could apply to the single genus *Mycterosaurus* and name the remaining slender Neovaransia as a more basal branch. The term “Mycterosaurinae” was introduced for *Mycterosaurus* and *Mesenosurus* (Reisz and Berman 2001), but defined as the

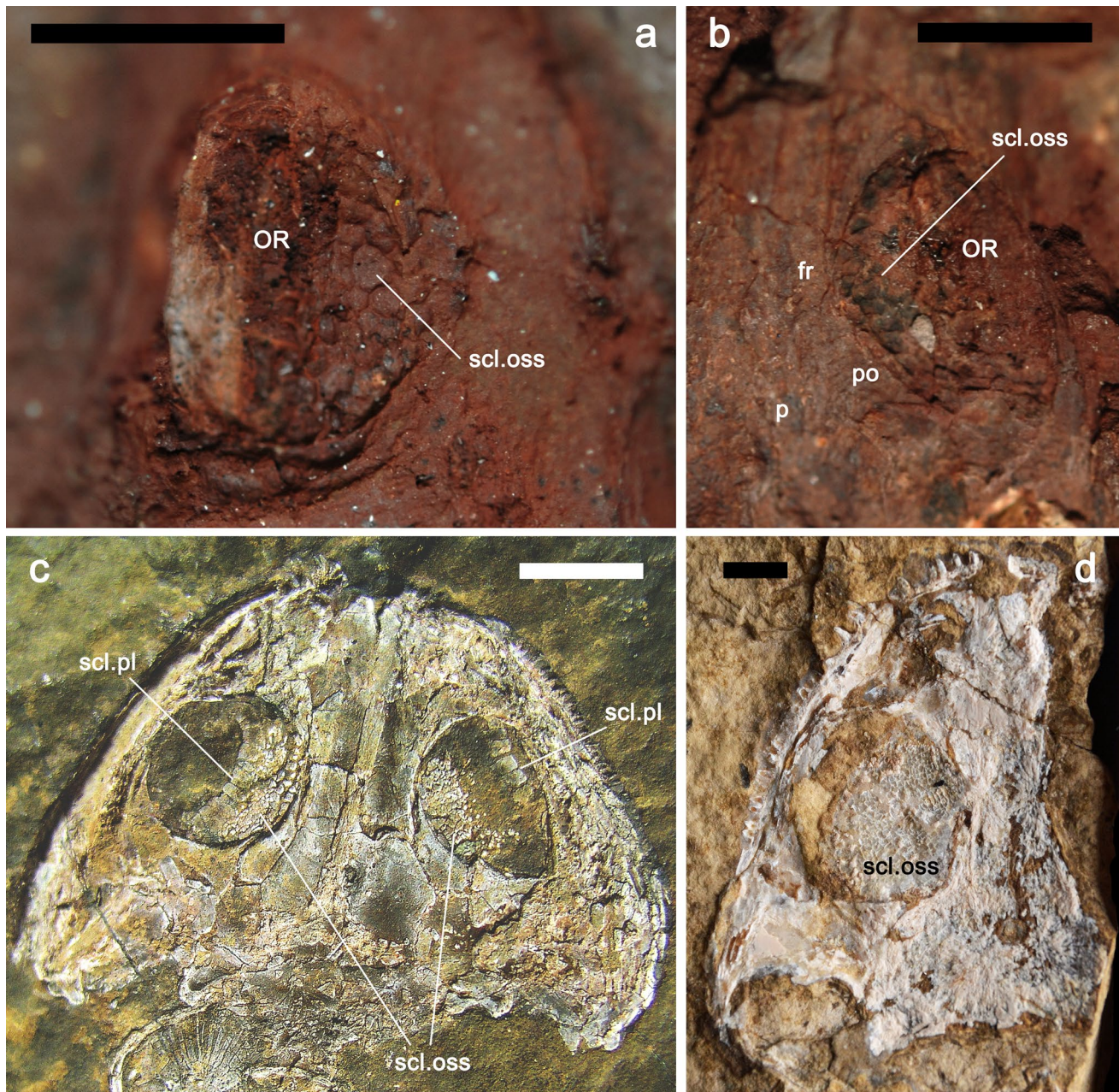


Fig. 26 Lid ossicles in various tetrapods. **a** Close-up of MNC-TA1045 of *Ascendonanus nestleri* gen. et sp. nov.; **b** same taxon, MNC-TA0924 (holotype); **c** skull of the micromelerpetontid *Branchi-erpeton amblystomus* (Credner, 1881) from the Sakmarian of Niederhäslich, Germany, holotype SNSD 320. Both the rhomboidal plates of the sclerotic ring and additionally the polygonal lid ossicles are

preserved in the large orbital fenestra (Werneburg 1991); **d** skull of the amphibamid *Eoscopus lockardi* Daly, 1994 from the Virgilian of Greenwood, Kansas, NHMS-VC 42 (see Werneburg 1993). The polygonal lid ossicles almost entirely fill the oval orbital sac. All scale bars measure 5 mm

sister taxon of Varanodontinae (Modesto et al. 2001). Due to the new relationship of both genera, “Mycterosaurinae” would turn paraphyletic, monogeneric or more inclusive. Therefore, the original definition of “Mycterosaurinae” without the eponymic *Mycterosaurus* is replaced by the new combination Mesenosaurinae. Some similarities

between *Mycterosaurus* and *Mesenosaurus* are explainable as symplesiomorphies.

Mesenosaurines share some synapomorphies, such as a squamosal posterodorsal process (56; shared with *Ascendonanus*, Caseasauria and others), tabular posteromedial process (65; unambiguous and unequivocal), long hind

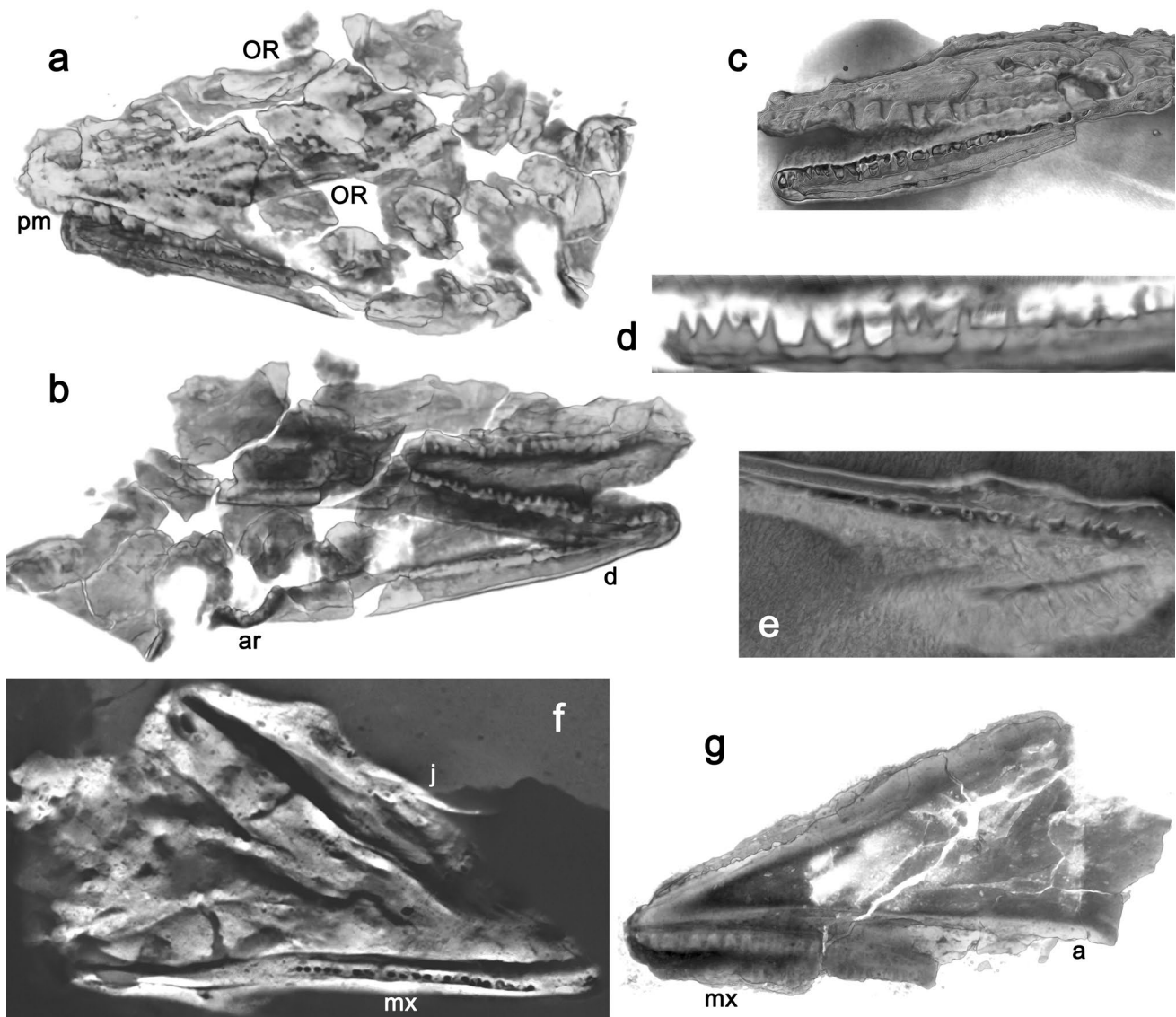


Fig. 27 Micro-CT images of *Ascendonanus nestleri*, gen. et sp. nov., skulls before preparation. **a–e** MNC-TA0924 (holotype); **a** in dorsal aspect; **b** oblique ventral aspect, exposing the articulated mandible; **c** left lateral aspect, with distinct hollows marking marginal tooth positions; **d** left dentary ramus; **e** dentary tip in dorsal aspect; **f** MNC-TA0906, merged images of palatal view; **g** MNC-TA0269, ventral aspect on right maxilla and complete mandible. For scaling compare Figs. 17, 21 and 23 of this article

limbs (143) and a stout calcaneus (176; shared with certain varanodontines).

An unnamed mesenosaurine from the early Sakmarian aged Goldlauter Formation of the Thuringian Forest Basin (Spindler and Werneburg 2016) plotted sometimes more basally than *Mesenosaurus* from the Krasnoschellie Formation, Biarmian (Kazanian) or lower Tatarian (Guadalupian, Mezen River Basin) in preliminary tests. In the majority of produced trees, the unnamed Thuringian mesenosaurine formed the sister to *Mesenosaurus*. However, it is well diagnosable and geologically much older than *Mesenosaurus* (Fig. 31). Both forms are grouped by a radius that is shortened with a degree that is unique to the included

synsids (158), along with several proportional features. The unnamed Thuringian mesenosaurine exhibits a larger and dorsally directed pubic tubercle (138), whereas *Mesenosaurus* is autapomorphic in a low ungual flexor tubercle (149) and a slender ulnare (162).

Gondwanan varanopid

So far, no pelycosaur-grade synsids have been discovered outside North America or Europe, except for six discoveries of lightly built varanopids from the South African Karoo Basin. Usually, these were assigned to “Mycterosaurinae” (Online Resource 1: Fig. A2), with some discussion about

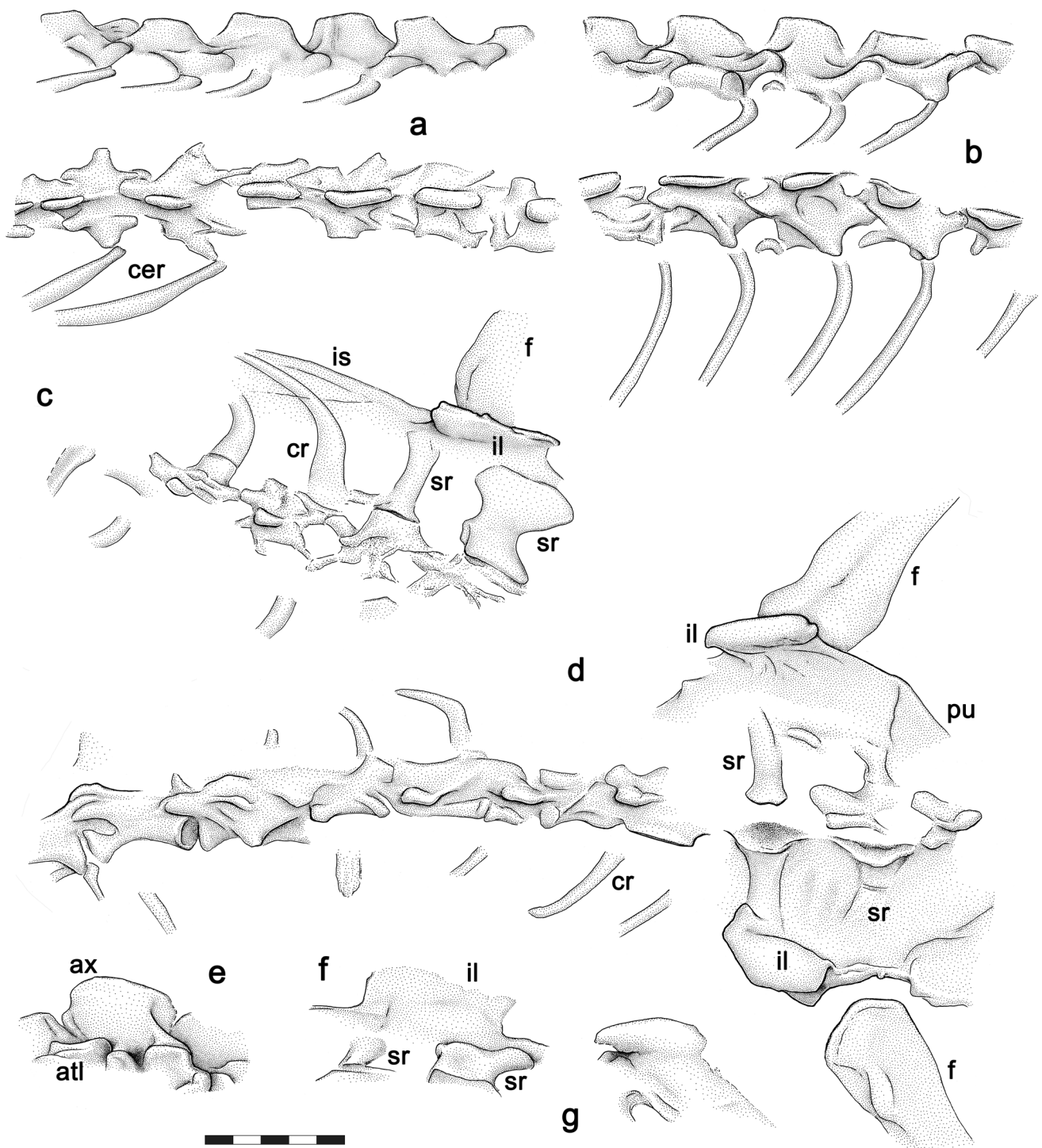


Fig. 28 Postcranial elements of *Ascendonanus nestleri*, gen. et sp. nov., drawn from silicon casts. **a** MNC-TA0269, cervical column in right lateral and dorsal view; **b** MNC-TA0906, anterior thoracal column in right lateral and dorsal view; **c** MNC-TA0269, hip region in

dorsal aspect; **d** MNC-TA0906, sacrum and proximal caudum in dorsal view; **e** MNC-TA0924, atlas-axis region in left lateral aspect; **f** and **g** left ilium in medial aspect, MNC-TA0269 and TA0906, respectively. Scale bar measures 5 mm

the genus *Elliotsmithia* (Modesto et al. 2001; Reisz and Dilkes 2003). As explained in the introduction to Online Resource 3, the present study aims to question some

taxonomic designations and to include all remains specimen-wise for the first time. It showed that the Gondwanan mesenosaurines form a certain subclade, which is not surprising

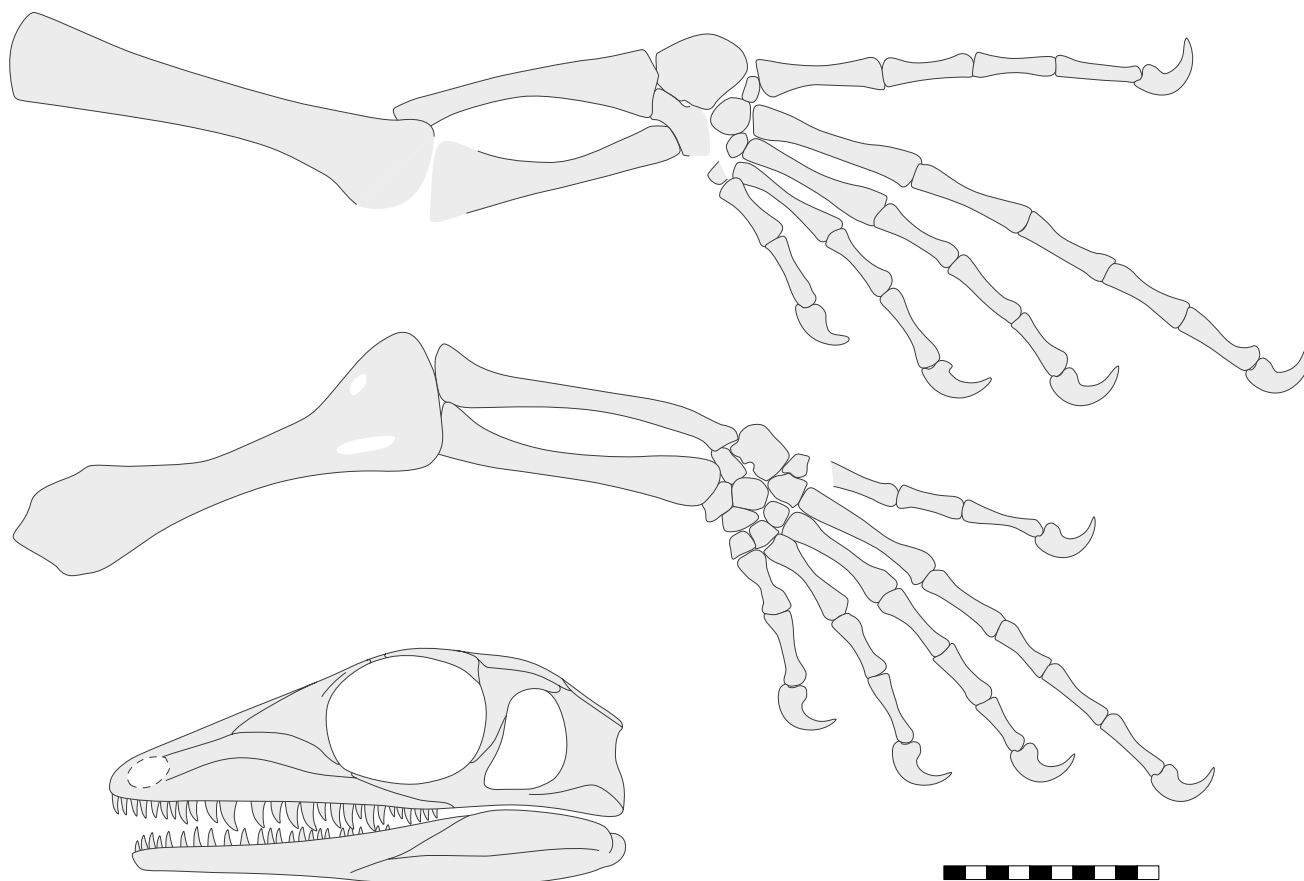


Fig. 29 Reconstructed skeletal complexes of *Ascendonanus nestleri*, gen. et sp. nov., showing the known parts of the dermal skull in lateral view and extremities. The skull drawing is based mainly on the

holotype MNC-TA0924, eliminating substantial compaction that effected the cranial region. Drawn to same scale; scale bar measuring 10 mm

with respect to their spatiotemporal occurrence. Earlier workers had partially prepared this grouping (Campione and Reisz 2010; Brocklehurst et al. 2016). The first assumption regarding this taxonomy goes back to Watson (1957) at least, who reconstructed a close relationship between *Mesenosaurus* and a lineage comprising *Anningia*, *Elliotsmithia* and *Heleosaurus* (altogether considered to be close to the parareptilian clade Millerettidae). In the present study, all South African mesenosaurines are combined within a clade, introduced as Afrothyra.

The internal resolution of Afrothyra is hampered by greater matrix gaps. Reisz and Modesto (2007) discussed whether *Elliotsmithia* and *Heleosaurus* might be identical, based on the same host formation and the presence of osteoderms. Botha-Brink and Modesto (2009) found no striking support for this consideration. However, their assignment of the family find SAM-PK-K8305 to *Heleosaurus* was premature even under the state of the art at their time.

Justification for a specimen-based analysis of the South African varanopids is explained in Online Resource 3, offering seven general varanopid traits of *Anningia*. Since no tree

hypothesis could resolve the internal relationships of Afrothyra (Fig. 30), a closer discussion is needed. In Table 1, the coded observations of certain specimens that yield distinction from one another or other varanopids are provided. The diagnosis of Afrothyra counts for two strong synapomorphies, being the presence of osteoderms (1; unambiguous and unequivocal) and a long postorbital-squamosal contact (48). As weaker synapomorphies from the reconstructed tree, great canines (31), a postorbital-supratemporal contact (49), as well as six isolated codings concerning the forelimb of SAM-PK-K8305 could possibly contribute to this diagnosis.

The family find SAM-PK-K8305 is grouped with *Anningia* on the basis of the apomorphic condition of a flat coronoid region (89), whereas SAM-PK-K8305 is unique in the presence of an ‘otic notch’ (54; shared with *Ascendonanus* and Caseasauria). In combination, *Anningia* could be valid, with one distinction and, reciprocally, one accordance with each SAM-PK-K8305 and *Elliotsmithia*. Additionally, *Anningia* is about as large as varanodontine varanopids (Fig. 32), showing a clear distinction from all other

mesenosaurines (for further comments, see Online Resource 3). However, no unquestionable apomorphy can be listed for *Anningia*, probably leaving this taxon to be a nomen vanum, as suggested by Reisz and Dilkes (1992), if not counting its huge size as a striking autapomorphy.

Anningia was declared a nomen vanum based on the "inability to identify or diagnose this taxon" (Reisz and Dilkes 1992: 1607), although a differential diagnosis could have been offered, if it had been compared to other specimens. For justification, Mones (1989) was cited, saying that this status applies to names based on types that are inadequate for a definitive diagnosis. What Reisz and Dilkes (1992) left out is another, independent issue: "The term should not be applied previous to a revision of the type material, original diagnosis, and specimens of closely related taxa" (Mones 1989: 233). At this time, it was not possible to name a certain taxonomic context to include *Anningia*, which is an inherent issue. Reisz and Dilkes (1992) already suggested *Elliotsmithia* to be a potential closer relative. The revision of true relatives started with Reisz et al. (1998), followed by the research history as listed in Online Resource 1. Thus, according to Mones (1989), the decision of Reisz and Dilkes (1992) was vague and should have been declared obsolete in subsequent studies. At no time was *Anningia* necessarily a nomen vanum. Today, the status designation nomen vanum is not in use anymore.

SAM-PK-K8305 is distinct from *Heleosaurus*, to which it has previously been assigned, in four characters (2, 13, 89, 102), and from *Elliotsmithia* in even more. Since it can be distinguished from its supposed closest relative *Anningia* by the presence of an 'otic notch' even in the unquestionable adult (Botha-Brink and Modesto 2009: fig. 2A), it deserves a new designation. SAM-PK-K8305 is becoming a holotype and hereby renamed as follows.

(unranked) **Synapsida** Osborn, 1903

Family **Varanopidae** Romer and Price, 1940

(unranked) **Neovaranopsia** comb. nov.

Subfamily **Mesenosaurinae** comb. nov.

(unranked) **Afrothyra** comb. nov.

Microvaranops parentis gen. et sp. nov.

ex *Heleosaurus scholtzi* Broom, 1907 (assigned by Botha-Brink and Modesto 2009)

Figure 32f

Etymology. Combining the genus designation *Varanops* ("monitor face") as being eponymous for the clade, with the prefix for "small;" epithet referring to the obvious preservation of parental care (Botha-Brink and Modesto 2007).

Holotype and only specimen. SAM-PK-K8305, a skeletal aggregation containing one grown and four immature individuals.

Locality and horizon. Beukesplaas farm, Cape Province, South Africa; *Tapinocephalus* Assemblage Zone, Abraham-skraal Formation, Beaufort Group, Middle Permian (Gadalupean), Karoo Basin (Botha-Brink and Modesto 2007, 2009).

Diagnosis. Small varanopid with dorsal osteodems and long postorbital-squamosal suture, therefore matching the diagnosis of *Afrothyra*, but with unserrated teeth and a flat coronoid region, distinct from *Heleosaurus* in lacking the shortened skull (less than the length of eight dorsals in *Heleosaurus*), distinct from *Heleosaurus* and *Elliotsmithia* in lacking skull ornamentation.

BP/II/5678, originally determined as *Elliotsmithia* (Modesto et al. 2001), is distinct from *Microvaranops* and *Elliotsmithia*, but lacks any autapomorphy. As there is no obvious distinction from *Heleosaurus*, BP/II/5678 can tentatively be assigned to this genus. Both finds are grouped because of the weak diagnostic of a tall axis spine (106), representing an apomorphy that is homoplastic with *Varanodontinae*. Additionally, an anteriorly short jugal allowing for an orbital contribution of the maxilla is present in both, although shared with *Elliotsmithia* (Fig. 32). The holotype of *Heleosaurus* (Carroll 1976) lacks a certain diagnosis itself, as no other afrothyran ischium outline (141) could be coded. Therefore, the combination with BP/II/5678 probably yields the only chance to provide a diagnosis for *Heleosaurus*.

The youngest varanopid SAM-PK-K10407 does not exhibit any distinction from *Elliotsmithia*, the holotype of *Heleosaurus*, or BP/II/5678. Although its stratigraphical distance might suggest a distinct genus, it does not show any apomorphy and thus cannot be determined on the genus level.

Regarding former discussions on the position of *Elliotsmithia*, a supposed varanodontine classification, as suggested by most analyses subsequent to Reisz et al. (1998), can be explained by erroneous codings (Online Resource 3: comments on excluded squamosal characters). Using corrected scorings (comments on characters 10, 45, 48), this genus never plotted among varanodontines in any preliminary test with the renewed data set, whereas it sometimes appeared to represent the basal-most member of *Afrothyra*. This supposed exclusion from derived *Afrothyra*s was weakly supported by two characters that are coded as unknown in *Elliotsmithia* (27; 31). Moreover, *Elliotsmithia* is the most autapomorphic (or at least deviant) OTU among known *Afrothyra*, exhibiting a slender posterior process on the postorbital (46), a maxilla reaching to the quadratojugal (62; shared with *Varanodontinae*, sensu this article),

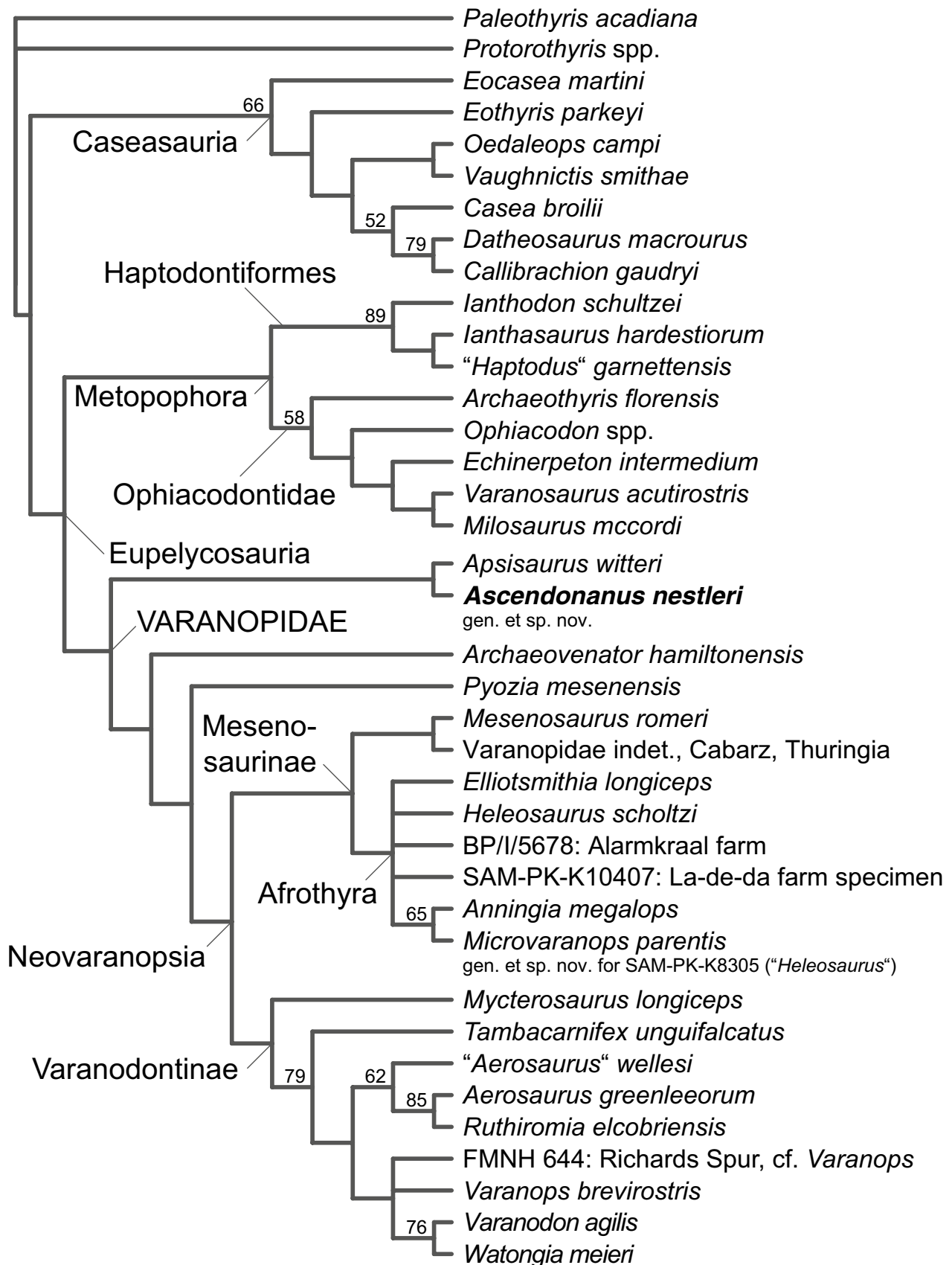


Fig. 30 Phylogenetic hypothesis for Varanopidae and close outgroups (heuristic search: strict consensus of 114 trees). New combinations introduced in the present study are Metopophora, Haptodontiformes, Neovaranopsia, Mesenosaurinae and Afrothyra. Tree length = 469, consistency index = 0.3859, retention index = 0.6201, rescaled consistency index = 0.2393; numbers on tree indicate bootstrap values after 100 replicates

opisthotic fused to the braincase (80; shared with Varanodontinae, sensu this article) and a low paroccipital process (81). The two mentioned resemblances with Varanodontinae are also seen in *Mycterosaurus*, probably indicating that *Elliot-smithia* and *Mycterosaurus* partially represent an initial stage of Neovaranopsia.

In total, no internal resolution is possible for Afrothyra. Nomenclatural validity is given for *Microvaranops*, *Elliot-smithia* and possibly for *Heleosaurus*.

Varanodontinae

The derived clade of Varanodontinae shows some parallelism with caseids and ophiacodontids in certain characters, which is why the entire family Varanopidae caused some confusion regarding its phylogenetic position at a time when it was known based on varanodontines only (Online Resource 1: Fig. A2). The increasing knowledge of basal varanopids now gives the chance to connect this clade more closely to the base of amniotes. The definition of Varanodontinae was first introduced by Reisz and Berman (2001; paralleled by Modesto et al. 2001).

The present analysis with a corrected data set has shown that *Mycterosaurus* is the basal-most known varanodontine. After only few workers have figured out a more basal position for *Mycterosaurus* within "Mycterosaurinae" (Modesto et al. 2001, partly: fig. 8a; Sidor 2001; Benson 2012), this is the first time that this genus falls outside of former definitions. This genus somewhat represents an intermediate form between smaller varanopids and greater varanodontine top predators. The renewed diagnosis for Varanodontinae includes a secondarily enlarged skull (2), a maxillary tooth row that reaches to or beyond the posterior margin of the orbita (28), a maxilla that reaches the anterior terminus of the quadratojugal (62), fused postparietals (66), opisthotic fused to braincase (80), tall dorsal spines (111), laterally excavated neural arches (115), narrowed posterior margin of entepicondylar region (154) and a relatively broad femur (167). Nonetheless, the mesenosaurine traits like the short lacrimal raise the question of substantial parallelisms among neovaranopsian lineages. The phylogenetic analysis of Berman et al. (2014) possibly demonstrates a case of reversed polarization when stating an evolutionary row of '*Heleosaurus*,' *Elliot-smithia*, *Mesenosaurus* and *Mycterosaurus*.

Mycterosaurus exhibits a greater apomorphic nature shared with *Aerosaurus* or higher varanodontines than with

the admittedly similar *Elliot-smithia*. *Mycterosaurus* also shows some autapomorphic traits, such as a pronounced and dorsally directed pubic tubercle (138), a distal position of the *M. latissimus dorsi* attachment on the humerus (152; herein reconstructed as a parallelism to lineage of *Aerosaurus*) and a perforating foramen that does not incise the calcaneus (174). *Mycterosaurus* is precluded from more derived varanodontines by postcranial features only, counting short dorsal centra (108), deeper excavations on neural arches (116), dichoccephalous ribs (119; character history questionable) and broad humeri (155).

The supposed next higher side branch is *Tambacarnifex*. This genus can be diagnosed with a weaker tooth curvature (100) and alternation in neural spine broadness (114). Under the present tree hypothesis (Fig. 30), the node comprising all more derived varanodontines is based on scorings that are missing in *Tambacarnifex* (45, 90), whereas the character history of pronounced unguis flexor tubercles appears to be affected by major functional parallelism (149; strong tubercles shared by *Ascendonanus*, the Thuringian mesenosaurine, *Tambacarnifex* and *Varanodon*). Therefore, *Tambacarnifex* might plot this deeply because of its fragmentary preservation and predominantly postcranial comparisons, resulting in stem-ward slippage. There is no reason to exclude it from the node containing *Varanops* and *Watongia*. In fact, it cannot be distinguished from the indeterminate Richards Spur varanodontine at this time. The latter should not be assigned to *Varanops* (as tentatively suggested by Maddin et al. 2006) because of its different calcaneus morphology (176) and an autapomorphic basiptyergoid (excluded from the present character list). *Tambacarnifex* might be closely related to *Varanops*, as reconstructed by Berman et al. (2014), especially since an undescribed interclavicle has been collected from the Tambach Formation (Kungurian, Thuringia Forest Basin) that is indistinguishable from that of *Varanops* (Romer and Price 1940: fig. 21; pers. obs. F.S. 2015).

That *Aerosaurus* is less derived than *Varanops* and *Varanodon* has been accepted since Brinkman and Eberth (1983) and Reisz et al. (1998). Benson (2012) was the first to include both species of *Aerosaurus* along with *Ruthiromia*. Since then, it has been confirmed that *Ruthiromia* is in fact a varanopid, as suggested by the original description (Eberth and Brinkman 1983; tentatively classified as an ophiacodontid by Spielmann and Lucas 2010). However, Brocklehurst et al. (2016) found *Aerosaurus* to be paraphyletic, with the type *A. greenleeorum* closer to *Ruthiromia elcobriensis*. Whereas Benson (2012) had found support for the monophyletic status of *Aerosaurus*, the same changing results from the present analysis. In order not to cause additional potential for taxonomic revision, it is recommended to rename '*Aerosaurus*' *wellesi* by a new genus designation, instead of assigning *Ruthiromia* to *Aerosaurus* as a third species.

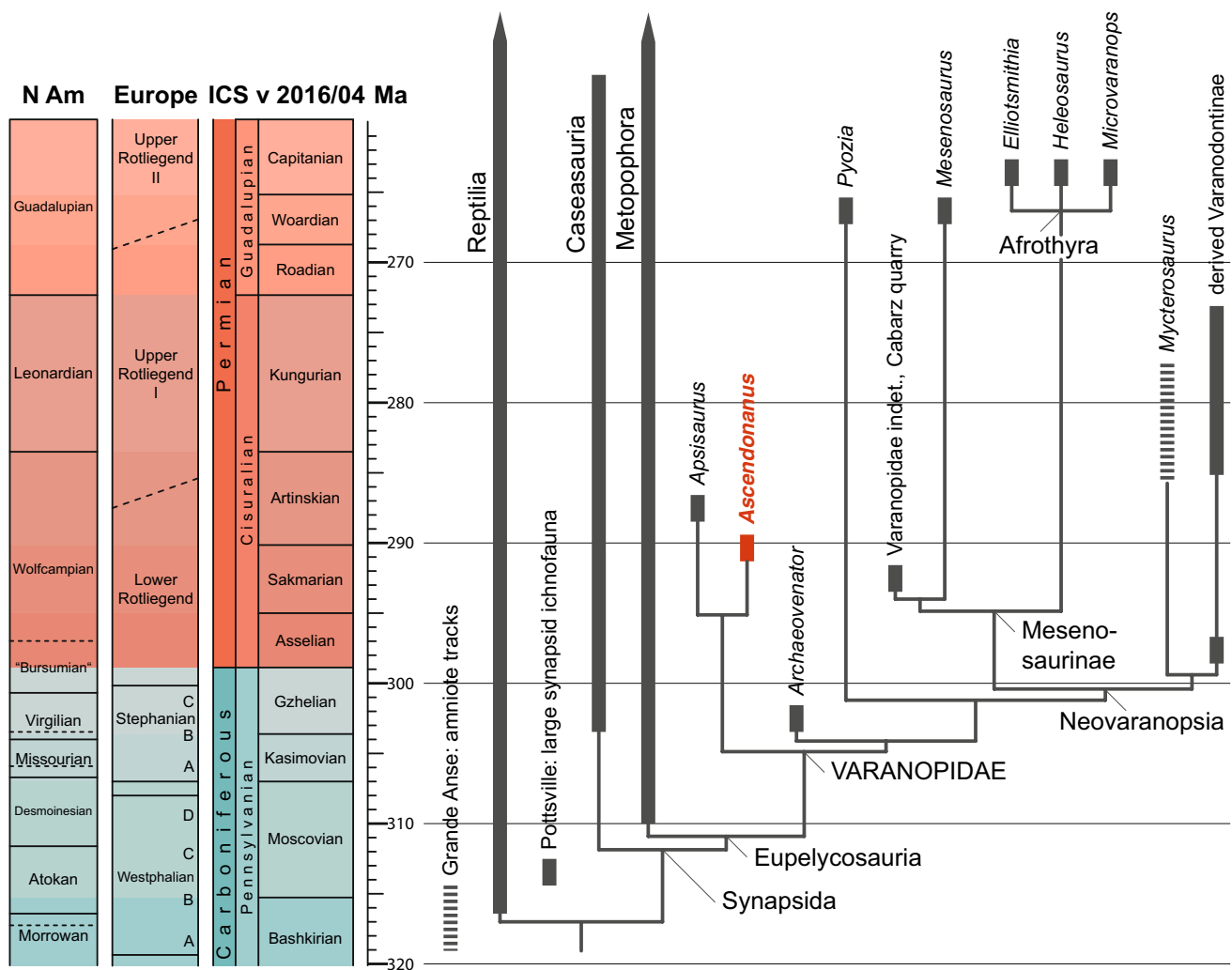


Fig. 31 Stratigraphically calibrated phylogenetic hypothesis for Varanopidae, revealing minor ghost lineages for varanopid origins, as well as the supposed *Apsisaurus-Ascendonanus* clade, and substantial gaps

for two mesenosaurine branches, being *Mesenosaurus* and the Gondwanan clade Afrothyra

As a condition, this would require a renewed study of *A. greenleeorum*, which is fragmentarily known and loosely documented in the literature (Romer 1937; Romer and Price 1940). The character list (Online Resource 3) contains several comments on all species in question that should be taken into consideration before renaming '*Aerosaurus*' *wellesi*. The three taxonomic units in question are herein defined as Aerosaurini, diagnosed by postcranial characters: a strongly concave anterior surface of the deltopectoral crest (151; unambiguous and unequivocal), distal position of attachment for *M. latissimus dorsi* (152) and conspicuous attachment for *M. puboischiofemoralis internus* (168). '*Aerosaurus*' *wellesi* might be autapomorphic in a sacrum containing three sacral vertebrae (121), a femur that is not much larger than the humerus (145) and a stout calcaneus (176), but all of these are unknown in *A. greenleeorum*. Nonetheless, a grouping of *A. greenleeorum* and *Ruthiromia* is appropriate based on a

pronounced triceps process on the coracoid (134) and the tubercle-like, posteriorly directed attachment for *M. latissimus dorsi* (153).

The most derived varanodontines form a clade that has never been debated. These forms are herein defined as Varanodontini. Their diagnosis is weak (ambiguous and equivocal), but convincing in the final tree hypothesis (Fig. 30), including a rather anterior position of the orbit (3), a high number of precaniniform teeth (29), a smaller pineal foramen (52), the flat coronoid region (89) and strongly uneven dimensions of sacral ribs (122). When including the indeterminate Richards Spur varanodontine, this diagnosis can be extended by adding a lacrimal facet on the maxillary dorsal lobe (23; unknown in Aerosaurini), a lateral supracanine buttress (24) and a ridge on the medial surface of the ilium (137). A robust and well-accepted node comprises *Varanodon* and *Watongia*.

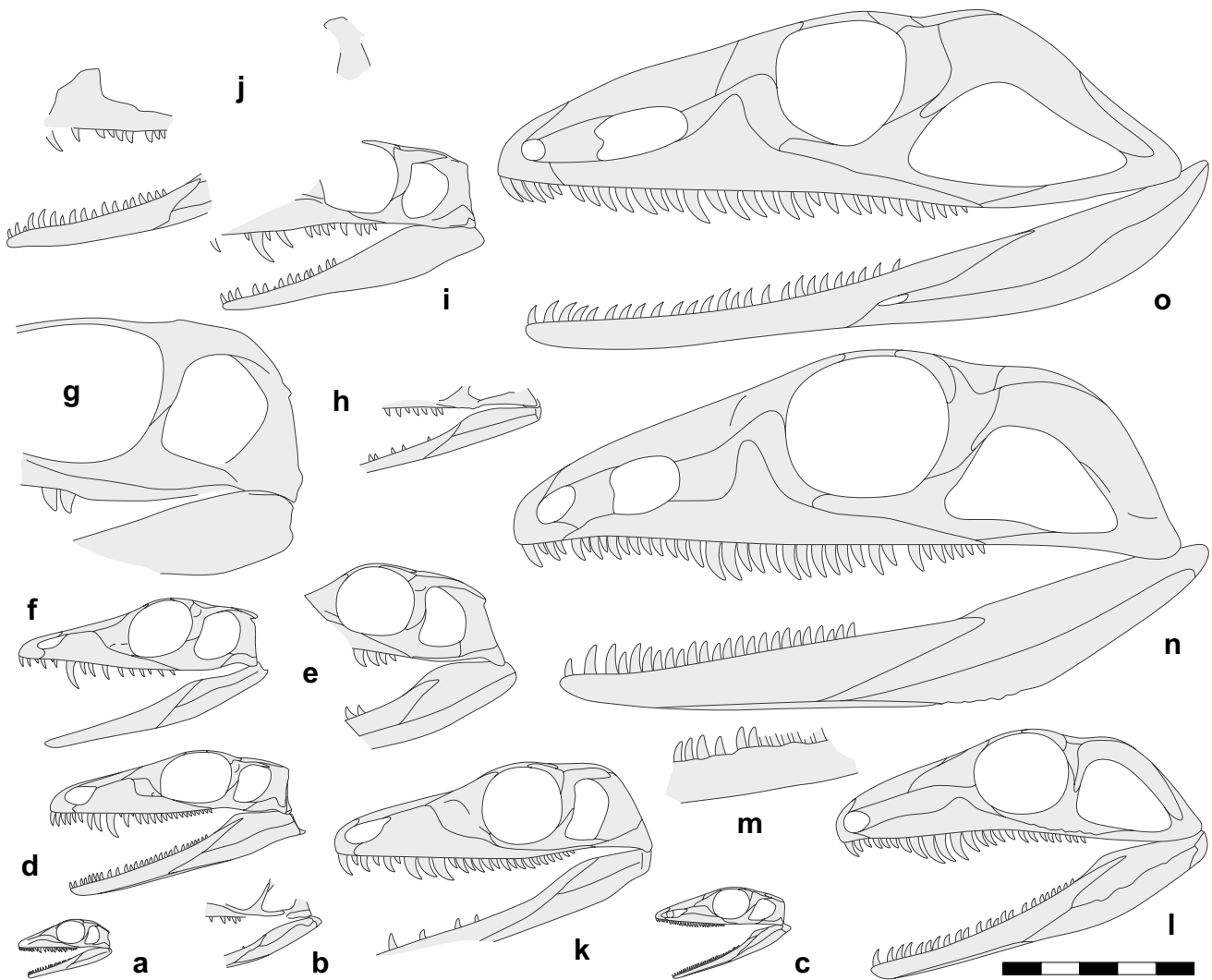


Fig. 32 Skull reconstructions of Varanopidae in left lateral aspect. **a** *Ascendonanus nestleri* gen. et sp. nov.; **b** *Apsisaurus witteri* (based on Laurin 1991 and Reisz et al. 2010); **c** *Archaeovenator hamiltonensis* (modified from Reisz and Dilkes 2003); **d** *Mesenosaurus romeri* (modified from Reisz and Berman 2001); **e** *Elliotsmithia longiceps* (based on Dilkes and Reisz 1996; Reisz et al. 1998; Modesto et al. 2001); **f** *Microvaranops parentis* gen. et sp. nov., ex *Heleosaurus scholzi* (based on Botha-Brink and Modesto 2009); **g** *Anningia megalops* (from Reisz and Dilkes 1992); **h** *Heleosaurus scholzi* (from Car-

roll 1976; Reisz and Modesto 2007); **i** BP/1/5678 (based on Modesto et al. 2001); **j** SAM-PK-K10407 (based on Modesto et al. 2011); **k** *Mycterosaurus longiceps* (modified from Berman and Reisz 1982); **l** '*Aerosaurus*' *wellesi* (modified from Langston and Reisz 1981); **m** *Tambacarnifex unguifalcatus* (from Berman et al. 2014); **n** *Varanops brevirostris* (modified from Reisz and Tsuji 2006; Campione and Reisz 2010); **o** *Varanodon agilis* (modified from Reisz and Laurin 2004). All drawn to same scale; scale bar measures 5 cm

From the present analysis, the following stronger synapomorphies can be listed: shallow neural arch excavations (116), elongated diapophyses (117), postzygapophyses contacting on the midline (118) and a reduced outer centrale carpi (164; see Online Resource 3 for revised interpretation).

Palaeoecologic implications

The five specimens of the new varanopid *Ascendonanus nestleri* were produced by the same tuff that also embedded

the Petrified Forest of Chemnitz. Their taphonomy is dominated by a rush tuff deposition, but under moderate temperatures, thus only weakly comparable to the coalification of the Permian amniote *Tridentinosaurus* from Italy (Leonardi 1959; Bernardi et al. 2014). Within this facies of Pompeii-like preservation, the Chemnitz varanopids are not only preserved in full articulation. They are also associated with much of their semi-aquatic environment. Since bigger amniotes as well as flying insects that might have inhabited this rich ecosystem are missing in this assemblage so far, it seems possible that these animals had already fled

before or were blown away during the first pulse of the S 5.1 eruption, respectively. Opposite to this, the escape instinct of *Ascendonanus* might have driven them up into the tree tops. In consequence, the close relation to higher trees conserved the preferred habitat. As an additional argument, the exceptional radian of unguis phalanges supports the interpretation of arboreality in *Ascendonanus*. Partly, the claws are upright in the tuff bed and preserve a curve of nearly 180°, while the remainders of the bodies are strongly flattened.

Increased unguis curvature is commonly accepted as an indication for climbing abilities of animals that do not perform a specialized raptorial use of claws. A comparison of *Ascendonanus* with other climbing amniotes is partially fruitful, whereas birds are ignored in this context for their flight abilities and deviant joint mechanics. Measurements in the newly described material are hampered by preservation, such as the exact direction of flattening or diagenetic stages of certain unguis elements. For example, some cases appear to preserve keratinous sheaths, further biasing the actualistic approach. Since the calculation recommended by Zani (2000) is inappropriate under these circumstances, unguis curvature was graphically estimated as the radian along the dorsal edge in lateral exposure. Although strongly influenced by preservation, *Ascendonanus* terminal phalanges exhibit a curvature of 2 to 3 rad. This contrasts with other pelycosaur-grade synsapsids, such as maximally 2 rad in *Haptodus*, 1.5 rad in *Dimetrodon* or less than 1 rad in *Varanops* (Maddin and Reisz 2007: fig. 4). The basal varanopid *Archaeovenator* is estimated with 1 rad at best (Reisz and Dilkes 2003: fig. 1). Outliers among Varanopidae are *Tambacarnifex* and an undescribed Thuringian form with about 2 rad in both. Extant climbing lizards (pers. obs. on Agamidae, Varanidae, Iguania) show a lesser curvature of the full claws, meaning that their unguis bones are even less curved.

Comparability with extant climbing reptiles that perform clinging is strongly biased by the immense role of soft tissues, like keratinous sheaths, toepads or adhesive lamellae (Zani 2000). In cases where tree climbers were distinguished from lizards perching in low vegetation, different trends were recognized, e.g., that some arboreal forms even show a decrease of claw curvature while growing longer and higher claws (Crandell et al. 2014). The impact of soft tissues might be responsible for a more complex variation of extant unguis curvature. Maybe, this pattern is not relevant in deep time; for example, the archosauromorph *Trilophosaurus* has been interpreted as a case of partial arboreal specialization (Spielmann et al. 2005) and exhibits an unguis radian similar to *Ascendonanus*, estimated to exceed 2.5 rad. More differentiation is reported from extant adaptations to microhabitat use, leaving claw lengths and heights as ecologic descriptors (Tulli et al. 2009). After all, there is substantial doubt on the concept of actualism in this case, since the quality of Paleozoic tree surfaces is not yet understood.

Beyond these independent arguments, the autopodial proportions should yield more confirmation for this reconstruction. In contrast with the oldest known certainly arboreal therapsid *Suminia* (Fröbisch and Reisz 2009: fig. 3c), *Ascendonanus* lacks greatly shortened phalanges, disproportionately elongated second-distal phalanges and any opposable medial digit. However, independently from absolute size the new varanopid shows strongly elongated and slenderer digital elements than any other pelycosaur-grade synsapsid (Fig. 33). Among basal varanopids, there is little comparison regarding the autopodia. Phalangeal slenderness in *Ascendonanus* might still reflect a plesiomorphic condition, contrasting with the distinctly broadened phalanges of larger varanopids. Nonetheless, the observed proportions of *Ascendonanus* even exceed those seen in *Archaeovenator*, in which, moreover, the unguis phalanges are markedly smaller. The phalanges of *Ascendonanus* are proportionally longer compared to metopodial elements than in *Archaeovenator*. Assuming an evolutionary continuity between Neovaranopsia and their common precursors with Caseasauria and Metopophora, their derived autopodial structure is apparently bound to a deviant locomotion. According to Fröbisch and Reisz (2009), the new varanopid does not belong to a grasping arboreal type, but to a clinging type, as confirmed by the elongated presacral column. This interpretation meets with the overall slim, elongate trunk and the extraordinarily curved claws, both strongly contrasting with many grasping climbers, such as *Suminia* (Fröbisch and Reisz 2011). As a slight overlap with the adaptations of *Suminia* and other climbing amniotes, the penultimate phalanges of *Ascendonanus* appear initially elongated in the second, the fifth and probably the fourth string, whereas phalangeal elongation is overall consistent throughout the manus and pes. It is difficult to quantify exact ratios because of preservation; therefore, Fig. 29 offers the best reconstruction. The only comparison among small varanopids is that the fourth toe of *Archaeovenator* lacks elongation of the penultimate phalanx. Among Paleozoic amniotes, *Ascendonanus* exhibits the largest autopodials compared to the entire limb lengths, with the exception of non-diapsid romeriid eureptiles, for which no ancestral comparison is possible so far.

An overview of early tree-climbing amniotes is provided by Fröbisch and Reisz (2009). Although their identification of the oldest known arboreal tetrapod is dated back with the present description, synsapsids in general might have played a major role in the establishment of arboreality, as further demonstrated by new discoveries (Sidor et al. 2016). However, there is minor reason to assume a stronger reptilian participation, beyond the Mesozoic examples listed by Fröbisch and Reisz (2009). As a common constraint, the terminal phalanges of amniotes usually form unguis, allowing for an invasion of plant-made grounds via climbing abilities. In the Paleozoic, the claw-coated unguis of synsapsids were

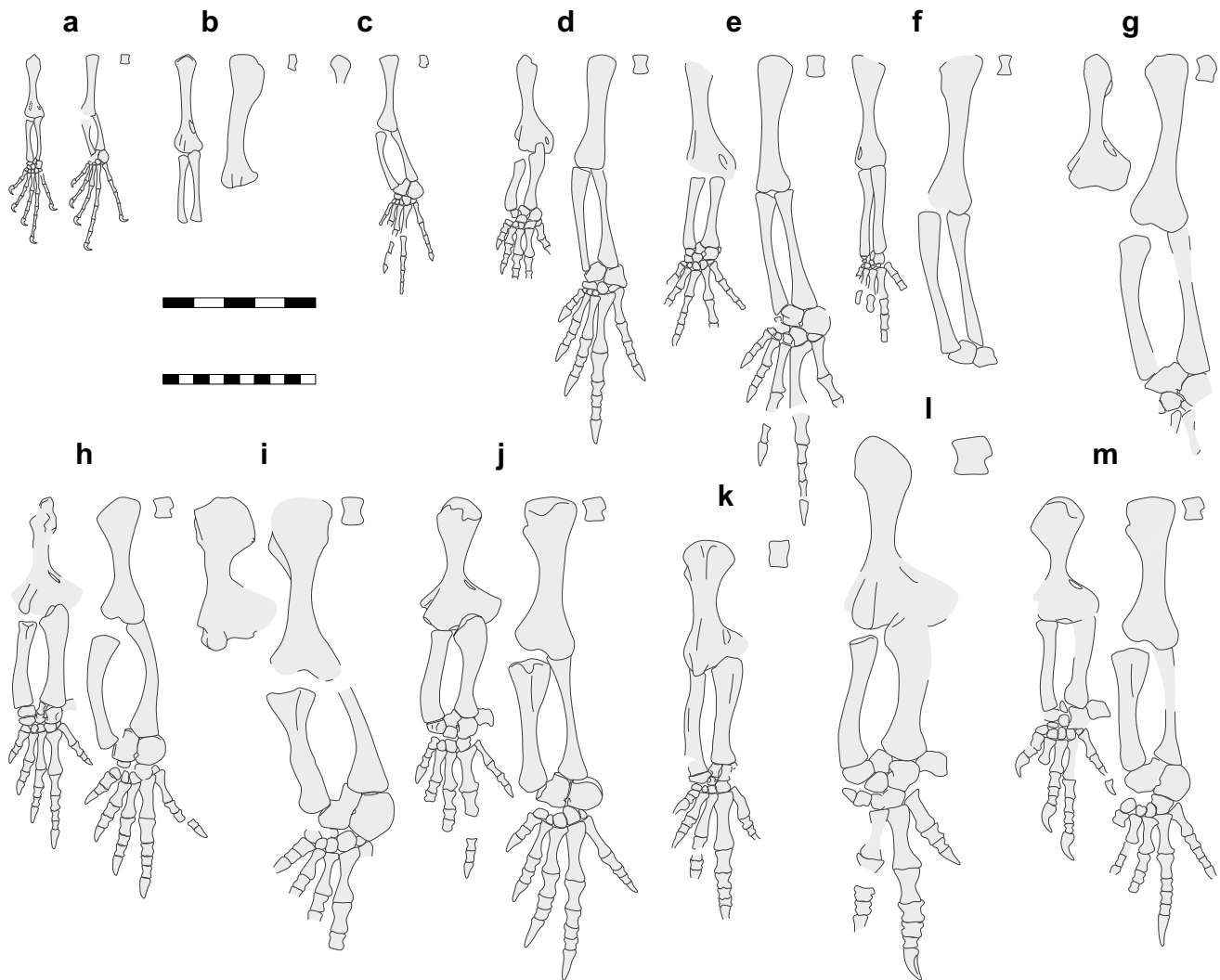


Fig. 33 Limb elements of known Varanopidae, with mid-dorsal vertebral centrum for size comparison. **a** *Ascendonanus nestleri* gen. et sp. nov.; **b** *Apsisaurus witteri* (Laurin 1991); **c** *Archaeovenator hamiltonensis* (Reisz and Dilkes 2003); **d** *Mesenosaurus romeri* (PIN 3713/1, PIN 3706/4); **e** Mesenosaurinae indet., Cabarz, Thuringia; **f** *Afrothyra* (combined from Carroll 1976 and Botha-Brink and Modesto 2009); **g** *Mycterosaurus longiceps* (Berman and Reisz 1982; Reisz et al. 1997); **h** *Aerosaurus wellei* (Langston and Reisz 1981; Pel-

letier 2014); **i** *Ruthiromia elcobriensis* (Eberth and Brinkman 1983; Spielmann and Lucas 2010; pers. obs. MCZ 3150); **j** *Varanops brevirostris* (Romer and Price 1940; Reisz and Tsuji 2006; Campione and Reisz, 2010; pers. obs. TMM 43628, MCZ 1926); **k** *Varanodon agilis* (Olson 1965; pers. obs. FMNH UR 986); **l** *Watongia meieri* (Olson 1974, Reisz and Laurin 2004); **m** *Tambacarnifex unguifalcatus* (Berman et al. 2014). Upper row compared to scale bar measuring 5 cm, lower row to scale bar measuring 10 cm (half the size of upper row)

mainly larger than those of reptiles proportionally. This circumstance probably favored an easier arboreal selection in synapsids. However, there were diapsid reptiles that might have been drawn into the arboreal lifestyle by the same (supposedly arthropod) food resources. Before the Triassic Kuehneosauridae evolved into gliding lizards, the late Permian Weigeltisauridae had invented a tree-down gliding. The interpretation of their arboreality bases on the investigation of Stein et al. (2008), who reconstructed a slowed-down parachute jump with a speed of several meters per second rather than a horizontal gliding flight ability. Gliding diapsids may have fed on insects collected during a climb up a tree stem,

until heading for the neighboring tree and using its lower branches to further brake their fall. Phalangeal elongation is weakly present in gliding diapsids (Colbert 1966; Evans 1982). With an ungual curvature of about 2 rad on the dorsal edge (Bulanov and Sennikov 2015: fig. 2; Evans 1987: fig. 10; Schaumberg 1986: fig. 1), weigeltisaurids show stronger curvature than most Palaeozoic reptiles. Because rocky environments play a minor role even for late Permian gliding reptiles, the presence of Permian arboreal reptiles is an appropriate conclusion.

Probably, reptiles even learned to climb antecedent to the Cisuralian varanopid *Ascendonanus*. The hyper-elongated



Fig. 34 Life reconstruction of a new varanopid synapsid, *Ascendonanus*, from the Permian petrified forest of Chemnitz, Germany. Body proportions, integument and arboreality were concluded from five specimens. Artwork by F. Spindler

phalanges of the late Pennsylvanian (Moscovian) protorothyridid *Anthracodromeus* have been discussed to indicate a climber (Carroll and Baird 1972: fig. 5e). Unfortunately, this reptile is poorly known, but its combination of hyperelongated digits with tiny unguals might indicate a third type of climbing mechanics besides grasping and clinging, being a spreading climber in a habitat dominated by plant axes.

All early arboreal tetrapods before the lineage towards the anomodontian *Suminia* were faunivorous. In their simple, conical tooth shape, basal varanopids including *Ascendonanus* resemble early reptiles more than Neovaranopsia. Thus, a clear distinction between the niches of small varanopids and those of *Lanthanolania* and other early neodiapsids, as stated by Reisz and Modesto (2007), cannot be confirmed.

Conclusions on the evolutionary history of the Varanopidae

A closer investigation of the epidermal structure of *Ascendonanus* and other basal synapsid material will be subject to a subsequent study. So far, it can be concluded that basal synapsid skin cover greatly resembles that of extant lepidosauromorph reptiles, confirming the plesiomorphic integumentary structure of Sauria (Lepidosauromorpha and Archosauromorpha) to be the common primary condition of Amniota. Although not surprising, the newly described

varanopid provides evidence for this plesiomorphic skin condition among a phylogenetic bracket that includes Parareptilia and (with the exception of derived Ichthyosauriformes) non-saurian Eureptilia, of which no preserved integument has been discovered up to now.

Not least regarding their integument, varanopids retained a resemblance with reptilian amniotes throughout their evolution, probably to a greater extent than other pelycosaur-grade synapsids. Mesenosaurinae were characterized as holding a niche of agile, small hunters, before they were displaced by neodiapsids (Reisz and Modesto 2007). Even more than the canine-bearing mesenosaurines, basal varanopids resembled various Paleozoic reptiles. With the knowledge of *Ascendonanus*, the disparity of varanopids has dramatically increased, introducing a dentition type that is intermediate between previously known basal forms and mesenosaurines and by presenting the first arboreal ‘pelycosaur.’ Strongly curved unguals in ground-living varanopids were described from *Tambacarnifex* (Berman et al. 2014) for the first time, followed by the Thuringian mesenosaurine, which furthermore is the oldest known biped (Spindler and Werneburg 2016). Therefore, the surprising degree of adaptability yields an explanation for the long persistence of varanopids as the apex predators that replaced Sphenacodontidae (Olson 1965; Reisz and Laurin 2004; Berman et al. 2014) or later co-existed with therapsid-dominated communities (Dilkes and Reisz 1996; Modesto et al. 2011). Based on the latest

Table 1 Observable traits of Afrothyra that might contribute to diagnoses

<i>Heleosaurus</i>	SAM-PK-K8305	<i>Elliotsmithia</i>	BP/1/5678	SAM-PK-K10407	<i>Anningia</i>
	osteoderms				
shorter skull	long skull				
skull ornamentation	skull lacking ornamentation	skull ornamentation			
	great canines				
	no frontal orbital lappet	frontal orbital lappet			
	slender postorbital bar	broad postorbital bar	slender postorbital bar		
	long postorbital-squamosal contact				
	postorbital contacts supratemporal				
	'otic notch'	no otic notch			no otic notch
maxilla not reaching quadratojugal		maxilla reaching to quadratojugal			
opisthotic not fused to braincase		opisthotic fused to braincase			
	tall paroccipital	low paroccipital			
coronoid eminence	coronoid region flat	coronoid eminence			coronoid region flat
serration	unserrated teeth	serration			
tall axis spine		axis spine low	tall axis spine		
	reduced entepicondyle ectepicondyle foramen long radius reduced olecranon reduced intermedium short manus				

research, varanopids cannot be described by narrow ecologic concepts any longer.

Taking into consideration that the Petrified Forest of Chemnitz is an exceptional environment in the currently sampled localities, it is indicative of how incomplete the ecologic spectrum of basal synapsids might be. Although demonstrating a real signal in early synapsid history, the diversity analysis of Brocklehurst et al. (2013: fig. 2b) reflects the general problem of paleo-environmental bias on the entire fossil record. The known diversity, and thus the correlating disparity, is the result of both the sedimentary window of fossil preservation and the diagonally crossing biome shift (Looy et al. 2014; Spindler 2015). Along with the overall rareness of relevant localities, the Chemnitz varanopids, which apparently were not rare in their habitat, help to point out that the previously reported adaptability of early synapsids was and probably will remain underrated when discussing their representativity in terms of true evolutionary history.

Based on the phylogenetic background, the knowledge of varanopid evolutionary history is more fragmented than in

other early synapsid subclades. The stratigraphically standardized tree (Fig. 31) contains some noticeable ghost lineages. The metopophoran sister group of Varanopidae has a minimum age of 310 Ma. There is no indication when the main diversification of basal varanopids occurred. A similar issue persists for the Caseasauria, of which the oldest representative *Eocasea* is from the same formation as *Archaeovenator* (Reisz and Fröbisch 2014). Since both basal-most branches of Synapsida appear later in the fossil record than more derived clades, there is no chance to reconstruct the ancestral stage of varanopid diversification. From the revised tree, the larger and more robust varanodontines appear mainly in the Artinskian, dating back their origin only by the Asselian form "*Aerosaurus*" *wellesi*. Mesenosaurinae are entirely Guadalupian in age after the preclusion of *Mycterosaurus* from "Mycterosaurinae," except for the recently identified Thuringian form. As the latter is very close to *Mesenosaurus*, the known Mesenosaurinae produce two major ghost lineages. Another one is caused by the basal form *Pyozia*.

In conclusion, a late Pennsylvanian radiation followed by a Cisuralian stability of clades might apply to Varanopidae similarly as to other early synapsids. However, the enormous fragmentation of their fossil record implies a paleo-ecologic explanation. As for the rare basal sphenacodontians, a climate-driven invasion to sedimentary basins matches well with the observation of the specialized *Ascendonanus* right within a rarely sampled environment. With respect to their potential affinity to extra-basinal stem habitats, varanodontines appear somewhat intermediate between Sphenacodontidae and Therapsida (Spindler 2014; 2015). With the exception of the Thuringian specimen, mesenosaurines show the same occurrence pattern as Therapsida. Basal Varanopidae such as *Ascendonanus* are singular finds that probably reveal the history of another long-lasting lineage after future finds.

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